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THE DESIGN AND ANALYSIS OF SALMONID TAGGING STUDIES IN THE COLUMBIA BASIN

Volume XII: A Multinomial Model for Estimating Ocean Survival from Salmonid Coded Wire-Tag Data

Technical Report

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THE DESIGN AND ANALYSIS OF SALMONID TAGGING STUDIES IN THE COLUMBIA BASIN

VOLUME XII

A Multinomial Model for Estimating Ocean Survial
from Salmonid Coded Wire-Tag Data

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Other Publications in this Series

Volume I: Skalski, J.R., J.A. Perez-Comas, R.L. Townsend, and J. Lady. 1998. Assessment of temporal trends in daily survival estimates of spring chinook, 1994-1996. Technical Report submitted to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 24 pp. plus appendix.

Volume II: Newman, K. 1998. Estimating salmonid survival with combined PIT-CWT tagging. Technical Report (DOE/BP-35885-11) to BPA, Project 91-051-00, Contract 87-BI-35885.

Volume III: Newman, K. 1998. Experiment designs and statistical models to estimate the effect of transportation on survival of Columbia River system salmonids. Technical Report (DOE/BP-35885-11a) to BPA, Project 91-051-00, Contract 87-BI-35885.

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Volume VI: Skalski, J.R., J.A. Perez-Comas, P. Westhagen, and S.G. Smith. 1998. Assessment of season-wild survival of Snake River yearling chinook salmon, 1994-1996. Technical Report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 23 pp. plus appendix.

Volume VII: Lowther, A. B., and J. R. Skalski. 1998. Monte-Carlo comparison of confidence interval procedures for estimating survival in a release-recapture study, with applications to Snake River salmonids. Technical Report (DOE/BP-02341-5) to BPA, Project 89-107-00, Contract 90-BI-02341.

Volume VIII: Lowther, A. B., and J. R. Skalski. 1998. Improved survival and residualization estimates for fall chinook using release-recapture methods. Technical Report (DOE/BP-02341-6) to BPA, Project 89-107-00, Contract 90-BI-02341.

Volume IX: Townsend, R.L., and J.R. Skalski. Submitted. A comparison of statistical methods of estimating treatment-control ratios (transportation benefit ratios), based on spring chinook salmon on the Columbia River, 1986-1988. Technical Report to BPA, Project 91-051-00, Contract 87-BI-35885.

Volume X: Westhagen, P., and J. R. Skalski. 1998. Instructional guide to using program CaptHist to create SURPH files for survival analysis using PTAGIS data files. Technical Report (DOE/BP-02341-4) to BPA, Project 89-107-00, Contract 90-BI-02341.

Volume XI: Skalski, J.R., R.L. Townsend, A.E. Giorgi, and J.R. Stevenson. Sub-

mitted. Recommendations on the design and analysis of radiotelemetry studies of salmonid smolts to estimate survival and passage efficiencies. Technical Report to BPA, Project 89-107-00, Contract DE-BI79-90BP02341. 33 pp.

Other Publications Related to this Series

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Lowther, A. B., and J. R. Skalski. 1998. A multinomial likelihood model for estimating survival probabilities and overwintering for fall chinook salmon using release-recapture methods. Journal of Agricultural, Biological, and Environmental Statistics 3: 223-236.

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Smith, S. G., J. R. Skalski, and A. E. Giorgi. 1993. Statistical evaluation of travel time estimation based on data from freeze-branded chinook salmon on the Snake River, 1982-1990. Technical Report (DOE/BP-35885-4) to BPA, Project 91-051-00, Contract 87-BI-35885.

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Giorgi, A. E. 1990. Mortality of yearling chinook salmon prior to arrival at Lower Granite Dam on the Snake River. Technical Report (DOE/BP-16570-1) to BPA, Project 91-051-00, Contract 87-BI-35885.

Preface

During the 1990s, PIT-tag studies on the Snake and Columbia Rivers have provided an important new source of information on salmonid life histories. Results from these PIT-tag studies provide information on salmonid smolt travel times, in-river survival, and run-timing. Tagging data from 1997-1998 have generated for the first time reliable smolt survival estimates from releases at the head waters of the Snake River Basin through Bonneville Dam tailrace. These tagging results are providing key information on in-river survival trends and the performance of hydroproject mitigation programs. However, in-river smolt survival is only one component of overall salmonid life histories.

Information on early ocean survival of salmonids and the oceanographic factors influencing survival remains sparse. This situation persists despite over two decades of coded-wire tag (CWT) releases. The purpose of this report is to investigate a multivariate analysis of age-at-return data generated by CWT releases. The analysis will extract early ocean survival rates of coho salmon off the coast of Washington state and relate these estimates to oceanographic conditions. The CWT data are not sufficient to examine decadal shifts in ocean productivity and environment change. Instead, the CWT data will be used in an attempt to explain annual fluctuations in coho return numbers. The analyses will also examine the consistency of results across fifteen different hatchery locations. The goal of this report is to present an approach to the analysis of CWT that might provide expand over understanding of salmonid life histories during their ocean residence.

This report is one in a series of reports illustrating statistical methods for analyzing Columbia Basin tagging studies. The goal of this series is to present state-of-the-art statistical methods that can more properly and more efficiently extract information from salmonid tagging studies. The intent of this series is to provide quantitative guidance on the design and analysis of tagging studies to investigators interested in generating reliable information for the management of salmonid resources in the Northwest.

Abstract

The purpose of this report is to illustrate the development of a stochastic model using coded wire-tag (CWT) release and age-at-return data, in order to regress first year ocean survival probabilities against coastal ocean conditions and climate covariates. The model will make no prior assumption about the distribution, or value of the model parameters. Survival probabilities, regression coefficients and associated variances of the parameter estimates will be derived using maximum likelihood theory. The goal of this report is to demonstrate a new way of analyzing CWT data to investigate the effect of different ocean conditions on salmon survival. The methods will be illustrated using CWT data from fifteen coho hatchery stocks in Washington State from 1970 to 1991. Meta-analysis will be subsequently used to make broad regional inferences regarding the effect of climate conditions on marine survival of coastal coho stocks. Additionally, the report shows that by using both fishery and hatchery return data, calculations of fishing effort are unnecessary.

Executive Summary

Objectives

1. Develop a method of obtaining age two survival estimates using coded wire tag data (CWT) of hatchery fish. CWT data will be analyzed using a new maximum likelihood method developed in this report. The maximum likelihood model will analyze data on age-at-return from adults recovered in the fishery and at the hatcheries across brood years to extract information on ocean survival of coho smolts.

2. Find associations between the survival estimates obtained and ocean conditions during the first few months of ocean residence. Several of the ocean conditions examined will be similar to those used in other studies, such as coastal upwelling, sea surface temperature (SST) and the strength of the Aleutian Low pressure system, in order to compare how the results of the new method compare with the results of previous studies. However, upwelling conditions vary along the coast by location and both upwelling and temperature vary seasonally. Therefore, covariates will be examined that account for the seasonal differences in SST and upwelling, and the spatial differences in upwelling along the coast. One other factor that will be examined is a general index of climate conditions in the Northwestern region of the U.S.

Accomplishments

1. Development of a stochastic model to estimate coho marine survival to age two, using coded-wire-tag data

2. Identified significant relationships between ocean and climate covariates and early marine survival of coho salmon using coded-wire-tag data. Survival relationships were found to be reproducible across coastal hatcheries.

Findings

A significant quadratic relationship between two ocean condition covariates, June sea surface temperature and upwelling conditions, and early marine survival of coho salmon.

Management Implications

The benefits of this research include a more effective use of currently available CWT data in obtaining accurate and precise estimates of early ocean survival, by utilizing all of the available information contained with-in age-at-return data. Moreover, a better understanding of the factors effecting the variability in adult salmon return numbers that should aid resource managers in partitioning sources of salmon mortality between environmental and human-related effects.

By understanding how and which mortality factors influence adult salmon returns, resources for mitigation and salmon recovery can be best directed for the benefit of the fishery and the Pacific Northwest.

Recommendations for further research

The maximum likelihood models developed for the coho investigations should be adapted to chinook salmon analyses. Relationships between chinook salmon returns and oceanographic conditions should be investigated. Meta-analyses of ocean relationships should be expanded to enclude Oregon and Washington states and British Columbia.

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Acknowledgments

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Introduction

Overview

Declines in the numbers of returning adult salmon (genus *Oncorhynchyus)* in the Columbia River basin have been observed over the past decades. Conventional wisdom being that the effect of man-made and natural river conditions on juveniles are the sources of these declines. The majority of mitigation and research efforts on the Columbia River have focused on improving survival during smolt outmigration. Studies on the effect of river conditions on in-river survival have used downstream/upstream, treatment/control approaches to looking at adult returns, (Hillborn et al., 1993; Skalski et al. 1996). Specifically, they have done this by estimating survival as the ratio of relative adults returns of various treatment/control groups, then assessing the effects of the treatments and river conditions on survival. Recently, it was shown that the inferences drawn from these studies are very sensitive to the choice of down-river controls (Skalski et al., 1996).

Fishery researchers and managers have noticed considerable variability in the number of returns of adult salmon, not only in the Columbia River system, but also in other areas. Nickelson (1986) noted annual fluctuations in adult hatchery return numbers and catch abundances for Oregon coho salmon (*Oncorhynchus kisutch*) during the period from 1970 - 1982, independent of the number of hatchery smolts released. Widely differing adult return numbers could have their origin occurring anywhere during life history of the salmon, in either the freshwater or ocean phases. A study of coho and chum salmon (*O. keta*) from Carnation Creek on the west side of Vancouver Island indicated freshwater residence and ocean residence contributed equally to the overall variability in adults returns (Holby and Scrivener, 1989). In addition to inter-annual variability, fluctuations in smolt survival for different stocks within a species has been observed (Pearcy, 1992, Bradford, 1995).

Most, or all, of the studies in the literature (Gunsolus, 1978; Scarnecchia, 1981; Nicholson and Lichatowich, 1984; Matthews, 1984; Nickelson, 1986; Fisher and Pearcy, 1988; Beamish and Boullion 1993; Beamish 1993; Francis and Hare, 1994) have relied on observational data (such as catch and escapement data) rather than experimental data in attempting to explain interannual fluctuations in adult salmon returns. Therefore, controls for sources of variation such as between species, between stocks of the same species, and between habitats must come from the choice of data used in the analysis. Researches generally look at only one species at a time, by sometimes aggregating stocks or by combining hatchery reared and wild fish in the same analysis (Nickelson, 1986).

The purpose of this study is look at the oceanic factors effecting variability of adult salmon returns. While chinook (*O. tshawytscha)* are of primary importance on the Columbia River system, coho salmon will be the focus of this initial investigation. There were two reasons for the choice of coho for this investigation. First, by selecting coastal stocks, confounding influences of in-river survival could be minimized or eliminated. Second, coho salmon have fewer returning age classes than chinook salmon, and as a result the data are easier to analyze and interpret. In addition, some of the methods used to analyze coho salmon data could eventually be modified to accommodate adult return data of chinook salmon. In order to better understand which oceanographic effects to investigate, it will be necessary to understand coho ocean ecology and the climatic and physical oceanic conditions that would affect salmon survival. Also, past and present methods of estimating salmon survival will be examined, and new methods of analyzing currently available data will be discussed. A brief review of salmon life history is discussed first, followed by a review of the physical and biological conditions in the coastal area of Washington.

Coho Life History

Coho salmon are found to spawn in coastal streams of Washington State, and in tributaries of the Lower Columbia River (Groot and Margolis, 1991). Adults return to their natal streams in the fall to spawn, usually between October and December. Spawning at the hatcheries is usually occurs between November and January (Washington State Department of Fisheries form 152). Cohorts are referred to by the brood year, which is defined as the year the adults returned to lay the eggs (in the fall), even though actual spawning may occur in January. Freshwater residence lasts about 15 months after egg deposition, with outmigration or hatchery release of yearling smolts occurring in April and May after the second year. The year of outmigration is two years after the brood year.

Coho smolts enter the ocean in May and June. Hatchery coho appear to move swiftly through estuaries during outmigration (Pearcy and Fisher, 1988), perhaps due to their large size during outmigration (Pearcy, 1992). After outmigration, most coho spend one winter in the ocean, before returning to spawn in the fall at age three. Some coho mature early and return in the fall in the same year of their outmigration, as two-year olds. The vast majority of the early maturing fish are males, and are termed jacks. A small percentage of coho spend two winters in the ocean and return as four year olds.

Most studies point to the first few months of ocean residence as the period in which most ocean mortality occurs (Matthews and Buckley, 1976; Bax, 1983; Nickelson, 1986; Fisher and Pearcy, 1988; Holtby et al., 1990; Francis and Hare, 1994). While the first summer in the ocean is important to survival, the period shortly after ocean entry is perhaps the most critical to cohort survival, and is perhaps the time when cohort success is determined (Pearcy and Fisher, 1988; Holtby and Scrivner, 1989; Brodeur et al. 1992; Pearcy, 1992; Beamish and Boullion, 1993). Therefore, what follows is a discussion on the feeding behavior and location of juvenile coho shortly after ocean entry, a description of the ocean and environmental conditions juvenile coho are exposed to, and finally a review of previous studies on the effects of ocean/climate conditions on coho marine survival.

The location of hatchery coho from Washington during their first summer in the ocean seems to be in the coastal area of Washington. Pearcy and Fisher (1988) found that CWT tagged juvenile coho seemed to be in the general region of ocean entry during the first summer at sea, and were not highly migratory. They found Columbia River fish south of the river mouth in May and June, then further north later in the summer. Pearcy and Fisher (1988) hypothesized that small coho smolts were carried south by ocean currents early in the summer, and then as the fish grew and became stronger, they moved further north.

Feeding behavior during early ocean residence is critical because the transition to the marine environment places increased energetic demands on juvenile salmon (Leavings, 1992). Coho appear to utilize different prey at different times of the summer, but overall had a diverse diet with several different prey categories including fishes, decapod larvae, pteropods, copepods and euphausiids (Brodeur and Pearcy, 1990). In May and June, larval fish are the most common prey item. In July and August, fish consumption declined and pteropods and euphausiids (invertebrates) were the major taxa consumed, while in September, fish prey were again dominant by weight (Brodeur and Pearcy, 1990; Broeduer et al. 1992). Juvenile coho displayed some variations in diet depending on where the juveniles were along the coast, with fish prey seemingly most important for coho off the coast of Washington (Brodeur and Pearcy, 1990). There has been speculation in the literature of differences between hatchery and wild fish in terms of feeding behavior, with hatchery fish perhaps having a different nutritional background (Leavings, 1992), or even a different image of what animals they recognize as prey (Brodeur et al., 1992).

Coastal Environment

The coastal ocean of Washington and Oregon is part of the coastal upwelling region of the northeastern Pacific Ocean (Bowden, 1983; Thompson and Ware, 1988). Upwelling occurs in the late spring and summer, when north to northwesterly winds moving parallel to the shore cause surface waters to move offshore (Ekman transport). The transported surface waters are replaced by cooler, nutrient rich waters from below to the surface layers. One effect of upwelling is cooler sea surface temperatures than in other coastal locations or in the mid-ocean at the same latitude. Winds favorable for upwelling, and hence upwelling, decrease further north (Schwing and Mendelssohn, 1997). Upwelling indices are calculated from surface winds rather than any physical measure in the water column, and the strength of upwelling is a function of the intensity and duration of favorable winds.

The driving mechanism behind the coastal winds inducing upwelling is the strength of the winter Aleutian Low Pressure system, which dominates the climate over the North Pacific. The Aleutian Low develops late in the year, and breaks down in the spring. Strong winter Aleutian Lows produce upwelling favorable winds in the center of the North Pacific, bringing nutrients to the surface, which are then transported east toward the west coast of North America (Beamish and Boullion, 1993), along with zooplankton (Brodeur and Ware, 1992). During periods of strong Aleutian Lows, the strong on shore surface flow and northward moving winds along the coast, causing downwelling. In the spring, the low pressure system weakens, and is replaced by an area of high pressure (Beamish, 1993; Robinson, 1994), producing more favorable northerly winds for upwelling. The change in wind patterns and hence between downwelling and upwelling conditions is known as the spring transition.

A consequence of upwelling is the introduction of nutrients which can be assimilated by phytoplankton, thus enhancing primary and plankton production in upwelling areas (Knuass, 1978; Robinson, 1994). Ware and Thompson (1991), using data from various upwelling conditions around the world, found that primary production was roughly proportional to the Ekman transport (upwelling), and that large fish stocks were down-current from the upwelling areas. The area of coastal Washington has enough light throughout the year for phytoplankton production, but is nutrient limited (Polovina, 1995), which explains the enhanced production during upwelling. The link between abiotic factors, such as climate and ocean conditions and pelagic fish appears to be through a pathway from nutrients to phytoplankton, to zooplankton, such a copepods, to larval fish and fish (Leavings, 1994; Robinson, 1994; McFarlane and Beamish, 1994). Several studies have linked increased plankton production (such as copepods) to increased fish production (McFarlane and Beamish, 1992; Robinson, 1994), and in particular, salmon production (Beamish and Boullion, 1993).

Previous Studies

Specific studies on the influence of ocean conditions on salmonid production are numerous, and coho salmon from Oregon and Washington are one of the most studied in the world (Pearcy, 1992). There have been a variety of methods for arriving at suitable estimates of salmon survival. Time series analysis of catch data has been the most widely used statistical method for looking at trends of salmon abundance (Matthews 1984; Beamish and Boullion 1993; Beamish 1993; Francis and Hare, 1994). Alternative indicators of survival have included using the number of returning jacks to predict catch and escapement of adults in the following year (Gunsolus, 1978), using catch and escapement numbers in conjunction with hatchery releases and stream production estimates (Nickelson, 1986), and the analysis of Coded Wire Tag (CWT) data using General Linearized Models (Cormack and Skalski, 1992; Hyun, 1996). Abundance or survival estimates from these methods have been correlated with North Pacific Ocean and climate conditions such as sea surface temperature, coastal upwelling conditions, and the strength of the Aleutian Low pressure system.

Numerous studies have examined the relationship between the strength of coastal upwelling and smolt survival and abundance (Gunsolus, 1978; Scanecchia, 1981; Nicholson and Lichatowich, 1984; Matthews, 1984; Nickelson, 1986; Fisher and Pearcy, 1988). A positive correlation has been found between cumulative upwelling and salmon survival (Gunsolus, 1978, Scarnecchia, 1981, Nickelson and Lichatowich, 1984 and Nickelson, 1986) and cumulative upwelling and salmon growth rate (Fisher and Pearcy, 1988, and Holtby et. al., 1990). The mechanism linking upwelling to salmon survival is enhanced plankton production and increased food supply, as a result of an increased nutrient supply (Leavings, 1994). Low primary and secondary production as a result of reduced upwelling would result in less food available for juvenile fish (Fisher and Pearcy, 1988), and perhaps even result in the possibility of food limitations during these periods (Brodeur et al. 1992). Several authors (McCarl and Rettig, 1983; McGie, 1984; Nickelson, 1986) have theorized that a decrease in upwelling during the spring and summer resulted in a decrease in ocean productivity and subsequently a decrease in salmon survival, as reflected in the observed numbers of adult returns.

One hypothesis for salmon survival in upwelling areas is the ocean productivity/ growth hypothesis, which states that salmon survival should be enhanced during year of strong upwelling due to faster growth rates as a result of better food sources (Pearcy, 1992). The productitivity/growth hypothesis was supported by Holtby et al. (1990) in a study of coho from Carnation Creek on Vancouver Island. The authors noted higher survival of coho with faster growth rates in years with ocean conditions indicative of strong upwelling, regardless of initial size, but higher mortality for smaller smolts in years of poor productivity because of a longer time spent at a smaller size. Size seemed to be more important to survival in years of high smolt mortality. Another hypothesis is the predation intensity hypothesis (Fisher and Pearcy, 1988) which links various levels of predation on salmon smolts to variability of ocean production. An increased level in predation on smolts could be due to either an increase in the number of predators or a lack of other food for predators. In the predation intensity hypothesis, smolt survival is assumed independent of smolt size and growth rates. The ocean productivity hypothesis assumes that predation is linked to size, but that predation rates may be variable (Holby et al., 1990). Fast growth rates would reduce the time the smolts are susceptible to predation, especially in the first month at sea (Nickelson, 1986; Pearcy, 1988; Holtby et al. 1990; Brodeur et al., 1992).

Fewer studies have pointed to a relationship between sea surface temperature (SST) and smolt survival. Negative correlations between coastal SST and smolt survival in the year of migration for both coho and chinook salmon have been reported (Nickelson, 1986; Hyun, 1996; Holtby and Scrivner, 1989). Holtby and Scrivener (1989) noted lower smolt survival during years of higher temperatures and low salinity. They also suggested variability in smolts survival was associated with variations in SST during the first few months of ocean residence. However, changes in survival seemed to be more related to changes in the distribution and abundances of predators than the actual changes in the physical environment. The authors also noted that the increase in predation could have been related to slower growth rates, which would increase the time smolts remain susceptible to predation. Nickelson (1986) reported that in years of strong upwelling conditions, smolt survival was negatively correlation with June SST. Additionally, McFarlaine and Beamish (1992) found an increase in year class abundance of sablefish (*Anoplopoma fimbria*) after extended periods of below average SST off the coast of Vancouver Island. Yet, because temperature is related to upwelling conditions (Knauss, 1983), it is possible that temperature is serving as another indication of upwelling strength. Trends in salmon production, as measured by catch data have been linked to climatic factors further off shore such as the intensity of the Aleutian Low Pressure system (Beamish and Boullion, 1993; Beamish, 1993; Francis and Hare, 1994).

In summary, marine survival of juvenile salmon has been positively correlated most often with upwelling, as measured by the total number of upwelling units over a specified time span, and negatively correlated with June SST. Trends in catch abundance has been associated with the strength of the wintertime Aleutian Low. The observational nature of the data used in past analyses makes the cause and effect relationship between oceanographic factors difficult to determine. Several theories have been proposed on the exact causes of smolt mortality, such as predation and growth rates, but thus far there has been little agreement on which theory provides the best explanation linking ocean conditions to smolt survival.

Goals of this report

The majority of the research indicates that the most important period for smolt survival is in the first few months of ocean life, and perhaps even the first month after outmigration. Finding associations between salmon survival and environmental conditions requires good, unbiased estimates of cohort survival during their critical period of survival. The data needed for survival estimates would include numbers of outmigrating smolts and the numbers of returning adults, or some other way to measure abundance of salmon after several months at sea. For these reasons, data on wild salmon runs do not necessarily provide the most ideal circumstances for the study of ocean survival (ie. poor estimates of outmigration and returning adults). Instead hatchery data will be used to obtain estimates of survival because the controlled conditions of a hatchery make it easier to obtain consistent estimates of salmon release and return numbers.

The method of obtaining age two survival estimates will use coded wire tag data (CWT) of hatchery fish. CWT data will be analyzed using a new maximum likelihood method developed in this report. The maximum likelihood model will analyze data on age-at-return from adults recovered in the fishery and at the hatcheries across brood years to extract information on ocean survival of coho smolts. Additionally, the report will also show that by using both fishery and hatchery return data, calculations of fishing effort are unnecessary.

The second goal of this report will be to find associations between the survival estimates obtained and ocean conditions in both the first month of ocean residence, and in the first few months of ocean residence. Several of the ocean conditions examined will be similar to those used in other studies, such as coastal upwelling, sea surface temperature (SST) and the strength of the Aleutian Low pressure system, in order to compare how the results of the new method compare with the results of previous studies. However, upwelling conditions vary along the coast by location and both upwelling and temperature vary seasonally. Therefore, covariates will be examined that account for the seasonal differences in SST and upwelling, and the spatial differences in upwelling along the coast. One other factor that will be examined is a general index of climate conditions in the Northwestern region of the U.S.

Data

Coded Wire Tag Data

Coded wire tag release and recovery data on coho salmon were obtained from the Regional Mark Processing Center, which is managed by the Pacific States Marine Fisheries Commission (PSMFC). Each year hatcheries tag a percentage of juvenile coho salmon with CWT tags, which are designed to remain with the fish for the remainder of the life of the fish. Coded wire tags are 1mm sections of wire encoded with a binary number, and placed into the nasal cavity of juvenile fish in order to track thier movement and survival patterns. The binary code on the tag identifies to the fish to a release group, and is referred to as a batch number. The adipose fin is clipped on fish tagged with a CWT, so that these fish can be externally identified.

Among the data recorded at the time the fish are tagged, and that are useful to this study include tag (batch) numbers, release numbers per batch, hatchery where the release occurred, date of release and brood year of the fish. Hatchery, brood year and date of release and release numbers are batch specific, and it is common for a hatchery to have several batch releases in a year.

Tags are recovered in the commercial and recreational fishery, and at the hatchery when the fish return as adults. In the commercial fishery only a fraction of the catch is sampled and checked for adipose fin clipped adults, because of the great number of fish caught. The number of fish with a CWT is recorded by batch as an observed return number. The observed number is divided by the sampling fraction to arrive at the expanded recovery number by the following equation,

$$E_i = \frac{O_i}{f_i} \qquad \text{(EQ 1)}$$

where O_i is the observed number of tags in a sample, f_i is the sampling fraction, and E_i is the expanded number, and i is the location where the tag is recovered. The total number of expanded recoveries per batch was the sum of expanded recoveries from all locations. The total number of expanded recoveries per batch and the year of recovery were used in the analysis. Tag returns from the recreational fishery are done on a voluntary basis, and are less accurate than commercial fishery and hatchery return data.

The objective in selecting hatcheries for the CWT data analysis was to minimize the time smolts spent in freshwater, both during outmigration and adult return, since assessing the effect of ocean conditions on salmon survival was the primary goal. Minimizing freshwater residence time means that most of the total survival can be attributed to ocean survival. Choosing hatcheries near the coast, or in the Lower Columbia area hopefully reduced the amount of variability in survival due to conditions that were not directly related to ocean residence.

Fifteen hatcheries were chosen, and divided into three regions, the Strait of Juan de Fuca hatcheries, Coastal hatcheries and Lower Columbia hatcheries. Hatcheries were put into the regions on the basis of the outmigration route, and where the smolts entered the ocean. The two hatcheries whose smolts entered the ocean in the Strait were put into that region, while the six hatcheries having an outmigration route on the coast or ocean entry just off the coast were placed in the coastal region. The lower Columbia region was designated for the seven hatcheries having migration routes through the Columbia River and ocean entry through the mouth of the Columbia River.

Hatchery locations are shown in Figure 1, along with the three regions. Brood

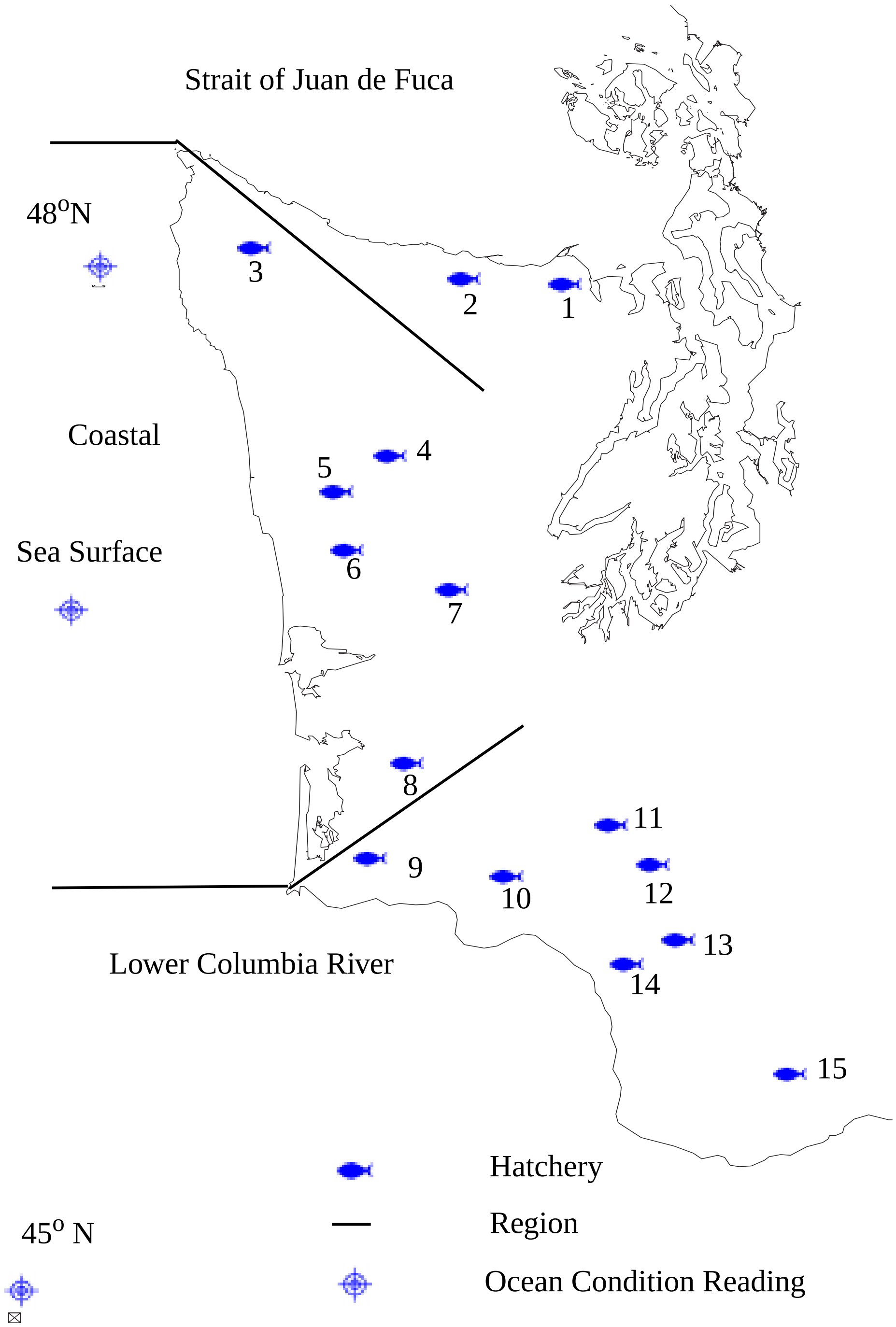

FIGURE 1. A map showing the locations of hatcheries used in the analysis and the regions in which they occur. The locations of upwelling condition observations and sea surface temperature (SST) observations are also shown. Numbers correspond to the hatcheries listed in Table 1

years and the total number of years of data for each of the hatcheries is given in Table 1. The minimum number of years of data required for the analysis was seven years. Although there are more hatcheries producing coho salmon than these fifteen, the others had fewer number of years with CWT releases. The earliest brood year where tagging took place was 1970, and the latest was 1991. Adult return data for brood years released later than 1991 were considered unreliable, because the records of adult returns beyond the 1991 brood year may be incomplete. A brood year of 1991 would have three year old returns in 1994 and four year old returns in the fall of 1995. Due to the time lag in reporting from provincial and state fisheries agencies on the observed and expanded numbers of adults in the commercial and recreational fisheries, 1995 is the last year with reliable return data.

Covariates - Ocean and Climate Conditions

Nine covariates were used in the analysis, each measuring a different aspect of ocean and climate conditions. Coho salmon smolts enter the ocean in the spring 15 months after the spawning of thier parents. The values of the covariates were for the first year of ocean residence. This means that for brood year of *i*, the covariate value is measured at year *i+2*, when the smolt entered the ocean were of interest. Two of the covariates were yearly indices of climate condition, two covariates were measures of sea surface temperature (SST), and five of the covariates were measures of coastal upwelling strength. Values for the environmental covariates from the year 1972 through 1993, and the corresponding brood years appear in Appendix B.

Sea Surface Temperature

Monthly sea surface temperatures (SST) were taken off of Copalis Beach in Washington State by NOAA observation ships, and is measured in degrees Celsius. Two measures of SST were used in the analysis of the effect of ocean temperature on marine survival of salmon. The June SST is the monthly average temperature for June in the year the smolts entered the ocean. The summer average temperature was the mean of the May through September monthly averages. The June temperature reflects the temperature when smolts from all regions have entered the ocean and encompasses the first full month of ocean residence. The Summer average temperature includes the temperature at the time of initial ocean entry in May, through the first five months of ocean residence.

TABLE 1. A table showing the coded wire tag (CWT) data by hatchery and the available bood years for each hatchery, and the total number of years of data. The last column refers to the location numbers on the map in Figure 1.

Region	Hatchery	Brood Years	Years of Data	Figure 1 number
Strait of Juan de Fuca	Dungeness Hatchery	1970 - 1972, 1975 - 1980, 1983, 1986, 1989, 1991	13	1
	Lower Elwha Hatchery	1978 - 1982, 1985 - 1989, 1991	11	2
Coastal	Soleduck Hatchery	1971, 1972, 1974 - 1976, 1980 - 1988, 1990, 1991	16	3
	Quinault Lake Hatchery	1977 - 1986, 1988 - 1991	14	4
	Quinault National Fish Hatchery	1973 - 1991	19	5
	Humptulips Hatchery	1980, 1982 - 1991	11	6
	Bingham Creek Hatchery (Simpson)	1971 - 1975, 1980 - 1991	17	7
	Willapa Hatchery	1971, 1974, 1980 - 1986	9	8
Lower Columbia	Grays River Hatchery	1974 - 1985, 1988 - 1991	16	9
	Elochomin Hatchery	1972, 1974, 1983 - 1985, 1988, 1989, 1990	8	10
	Cowlitz Hatchery	1972, 1980 - 1991	13	11
	Toutle Hatchery	1972, 1977, 1978, 1986 - 1991	9	12
	Kalama Creek Hatchery	1977, 1985 - 1989, 1991	7	13
	Kalama Falls Hatchery	1983 - 1985, 1988 - 1991	7	14
	Washougal Hatchery	1974, 1977 - 1982, 1988 - 1991	11	15

Upwelling Conditions

Recordings on the strength of coastal upwelling were taken from two areas off the coast, one from 45^{o} North latitude, and the other at 48^{o} North latitude. Upwelling conditions were given in terms of monthly averages and measured on the Bakun upwelling index, with units of metric tons/second/100 miles of coastline (Bakun, 1973), or a flow rate per length of coastline. Higher values of the index indicate stronger upwelling conditions, with positive values indicating upwelling and negative values indicating downwelling conditions. Data were provided through the NOAA data center, and were recorded by observations from ships. The locations were chosen to reflect the entire area juvenile coho from the selected hatcheries inhabit during the first year of ocean residence.

Three measures of upwelling conditions from the two locations were used in the analysis. As with temperature, the average June upwelling index from both the 45^{o} and 48^{o} were chosen to reflect the upwelling conditions during the first full month of ocean residence. The summer average upwelling covariate was the mean of the May through September monthly averages, again taken from both locations. Summer average upwelling covariate was a summary statistic reflecting the strength of coastal upwelling from the period the juveniles initially enter the marine environment, through the first several months of ocean residence.

The third measure of upwelling was a seasonal total of monthly average upwelling indices from March to September, inclusive, at both 45^{o} and 48^{o} North. Termed the cumulative upwelling index, this measure of upwelling is similar the that used in other studies (Gunsolus, 1978, Scarnecchia, 1981, Nickelson and Lichatowich, 1984 and Nickelson, 1986 and Hyun, 1996). This measure of upwelling may be thought of as indicative of the amount of nutrients put into the coastal environment for primary production. The covariate was used in the analysis as a way of checking the model to see if it would yield results similar to previous studies.

Northern Upwelling Extent

Another measure of upwelling used in the analysis measured how far north upwelling occurred during the month of June. During the winter months, downwelling occurs off the coast of Washington and Oregon, and changes to upwelling in the spring. However, this is not necessarily the case along the coast of British Columbia and southeastern Alaska where downwelling may continue through the summer. It is believed that as upwelling occurs further to the north in the spring and summer, favorable conditions occur for predators of juvenile salmon, and thus they may move north and out of the coastal Washington area.

Coastal upwelling data were taken at 3 degree intervals along the coast as far north as 54^o North, which is off the coast of Southeastern Alaska. The most northerly location of upwelling (positive index value) in the month of June was the basis for the covariate. A value of one (1) was given if the upwelling occurred at 48^o North, and downwelling occurred at locations north of 48^o. A value of two (2) meant upwelling was observed at 51^o North, (off the northern tip of Vancouver Island, British Columbia), but downwelling at 54^o North, and a value of three (3) was given for the covariate if upwelling occurred at 54^o North, the most northerly observation point.

North Pacific Index and Pacific Northwest Index

Both the North Pacific Index and Pacific Northwest Index are yearly measures of climate conditions. The North Pacific Index (NPI) was developed by Trenberth and Hurrell (1994) and is a measure of the circulation in the north Pacific designed to exhibit changes in the intensity of the winter Aleutian Low pressure system. The NPI is an average of sea level pressure in the area from 30 to 60^o N and 160^o E to 140^o W longitude, weighted by area, for the months November through March. Lower values imply lower mean sea level pressure over this area. Values range from a low of -5.82 millibars (mb) to 2.25 mb for the period 1972 to 1993, with a mean of -0.9383 mb.

The Pacific Northwest Index (PNI) is reflective of climate conditions and patterns in Washington State, both inland and on the coast. It is a yearly composite index developed by Ebbesmeyer and Strickland (1995) and uses three parameters from different locations in Washington. The parameters are 1) snowpack depth at paradise on Mount Rainier on 15 March of each year, 2) total annual precipitation at Cedar Lake in Washington State and 3) the average annual air temperature at Olga in the San Juan Islands. The index is a yearly average of the standardized values of the three parameters. Negative values signify a cooler, wetter than average year, and positive values indicate a warmer and dryer than average year. PNI values for the period from the earliest CWT release in the study, 1972, to the latest CWT release, 1993, ranged from a low of -1.39 (cool and wet) to a high of 1.42 (warm and dry), with an mean of 0.2746. All covariate values are given in Appendix B.

Methods

The approach to analyzing the CWT tag release and return data involved modelling the returns of all age classes using a multinomial probability model. Age class survivals and maturity rates were used to construct cell probabilities in the multinomial model and the age class return numbers were the cell counts. To assess the effect of ocean/climate conditions on first year ocean residence, first year ocean survival was modelled using a proportional hazards relationship, and regressed against ocean and climatic covariates. The model uses coho salmon rather than chinook, because fewer age classes (3 for coho, 6 for chinook) results in fewer cell probabilities and hence fewer parameters to estimate, since each cell probability incorporates several parameters.

The multinomial model used in the analysis is a process driven model. Figure 2 provides a schematic representation of the process being modeled. A cohort of tagged juveniles is released as yearlings (1.5 years of age) from a hatchery and outmigrants to the ocean. Some of these fish will survive the first six months in the ocean, and a fraction of these fish will reach maturity and either return to the hatchery, or be caught in the fishery. A proportion of the remaining fish will survive in the ocean to become three year olds. Of the surviving three year olds, most will either mature and return to the hatchery or be caught in the fishery. In some years, however, a small fraction will remain in the ocean, and return at age 4. The fishery and hatchery are the only places where tags are recovered.

The expected number of tag returns at each point where a fish may be recovered can be written in terms of the survival, maturity and catch probabilities. The parameters used in the likelihood model are defined below:

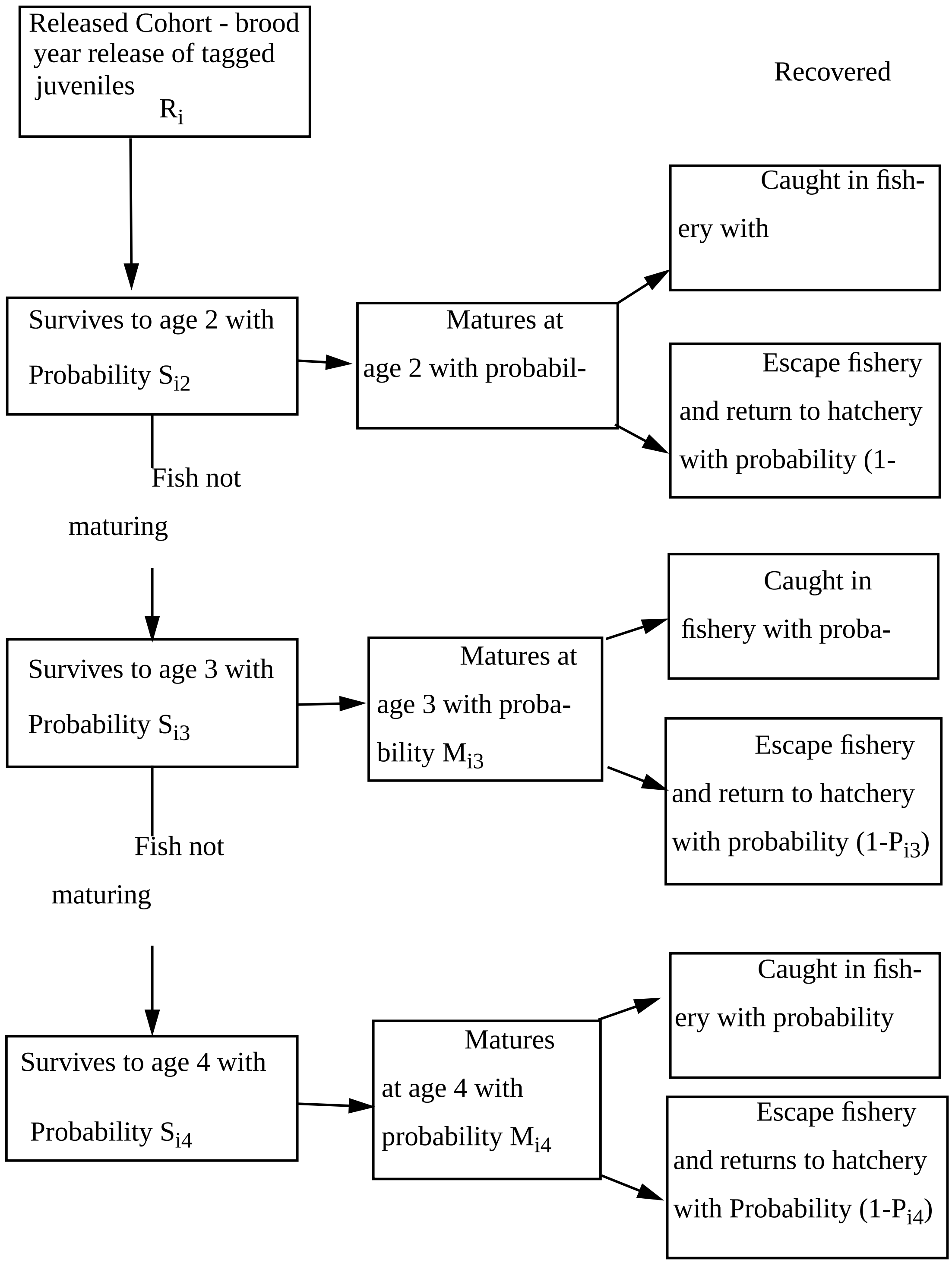

FIGURE 2. A diagram showing the process upon which the model is based, and the derivation of the cell probabilities for the analysis of coho CWT data.

R_i = total number of CWT marked smolts released from a hatchery for the ith brood year;

O_{ij} = number of CWT marked fish recovered in the fishery of the ith brood year of the jth age class;

H_{ij} = number of CWT marked fish recovered at the hatchery of the ith brood year of the jth age class;

S_{ij} = probability of a fish from the ith brood year surviving to the jth age class given survival to the j-1 age class;

P_{ij} = probability of being caught in the fishery at the ith brood year of the jth age class;

M_{ij} = probability of maturing at the jth age class for the ith brood year;

t_{ij} = number of expanded recoveries of CWT tagged fish from both the fishery and hatchery of the ith brood year in the jth age class.

The parameter M_{ij} encompasses not only the probability of maturing in the jth age class, but also the probability of reaching a size susceptible to fishing. Incorporating M_{ij} into the model is important because fish must be of a certain size to be recovered in the fishery. Thus, M_{ij} may also be thought of as the probability that the fish will be of a certain size or type so as to be seen in either the fishery or the hatchery.

The expected number of two year olds recovered in the fishery and hatchery can be expressed as $E(O_{i2}) = R_i P_{i2} S_{i2} M_{i2}$ and $E(H_{i2}) = R_i (1-P_{i2})S_{i2} M_{i2}$, respectively. The expected number of two-year old fish recovered from both sources is then:

$$\begin{aligned} E(H_{i2} + O_{i2}) &= R_i P_{i2} S_{i2} M_{i2} + R_i (1-P_{i2})S_{i2} M_{i2} \\ &= R_i P_{i2} S_{i2} M_{i2} - R_i P_{i2} S_{i2} M_{i2} + R_i S_{i2} M_{i2} \\ E(H_{i2} + O_{i2}) &= R_i S_{i2} M_{i2} \qquad \text{(EQ 2)} \end{aligned}$$

Similarly, for three years olds, the expected number of ocean and hatchery recoveries is expressed as $E(O_{i3}) = R_i P_{i3} S_{i3} S_{i2} M_{i2}$ and $E(H_{i3}) = R_i (1-P_{i3})S_{i3} S_{i2} M_{i3}$, respectively. The total number of three year old recoveries has expected value

$$E(H_{i3} + O_{i3}) = R_i P_{i3} S_{i3} S_{i2} M_{i3} + R_i (1-P_{i3}) S_{i3} S_{i2} M_{i3}$$

$$= R_i P_{i3} S_{i3} S_{i2} M_{i3} - R_i P_{i3} S_{i3} S_{i2} M_{i3} + R_i S_{i3} S_{i2} M_{i3}$$

$$E(H_{i3} + O_{i3}) = R_i S_{i3} S_{i2} M_{i3} \qquad \text{(EQ 3)}$$

The expected number of ocean and hatchery recoveries of four-year old coho may be expressed as $E(O_{i4}) = R_i P_{i4} S_{i4} S_{i3} S_{i2} M_{i4}$ and $E(H_{i4}) = R_i (1-P_{i4}) S_{i4} S_{i3} S_{i2} M_{i4}$, respectively. The expected number of total recoveries from both sources is then:

$$E(H_{i4} + O_{i4}) = R_i P_{i4} S_{i4} S_{i3} S_{i2} M_{i4} + R_i (1-P_{i4}) S_{i4} S_{i3} S_{i2} M_{i4}$$

$$E(H_{i4} + O_{i4}) = R_i P_{i4} S_{i4} S_{i3} S_{i2} M_{i4} - R_i P_{i4} S_{i4} S_{i3} S_{i2} M_{i4} + R_i S_{i4} S_{i3} S_{i2} M_{i4}$$

$$E(H_{i4} + O_{i4}) = R_i S_{i4} S_{i3} S_{i2} M_{i4} \qquad \text{(EQ 4)}$$

however, $M_{i4} = 1 - (M_{i2} + M_{i3})$.

Two important aspects of the above equations should be noted. The first is that by combining the recoveries from all sources the fishing effort, P_{ij}, drops out of the equation. Thus there is no need to calculate fishing effort in order to analyze the data. While this is not the first time total recoveries have been used in analyzing CWT data (Nickelson, 1986), it has not been shown in the literature formally, or proven that the fishing effort drops out of the equation when total recoveries are used. The number of tag returns will be modelled using a multinomial approach, with the survival and maturation probabilities used in the cell probabilities.

Some of the assumptions used in the CWT model were those universal to many mark-recapture models and some assumptions were specific to this model. The stochastic CWT model has the following assumptions:

1) the tag groups are representative of the population of inference,

2) all tagged fish had an equal probability of surviving and migrating back to the hatchery in a particular year,

3) release numbers of tagged smolts were known without error,

4) the numbers of recovered tagged fish for each tagging were correctly reported,

5) tag group numbers were correctly identified,

6) release groups were assumed closed to emigration and the number of tagged hatchery fish straying to the spawning grounds, an area where tags are less likely to be detected, was assumed negligible,

7) $M_{ij,}$ was assumed constant across all years for the same stock from a hatchery,

8) fish were not susceptible to being caught in the fishery until they have reached a certain size and,

9) fish caught in the fishery were a random sample of the fish migrating that year (i.e. no bias toward tagged fish in the fishery),

10) the fish inspected for tags in the fishery were a representative sample of all fish in the fishery and the fraction of fish sampled was known without error.

Tagged fish straying to other hatcheries was not considered a problem because fish are checked for tags at hatcheries and would therefore be recovered. Release numbers were not adjusted for tag loss in the analysis because the tag loss rates of the CWT tags are not estimated reliably, although the number of observed recoveries are adjusted slightly upward to account for unreadable tags, or tags lost during reading (Markey et al. 1989).

Using the expected values of tag recoveries for each age class, a multinomial model was developed. The likelihood model, where n is the number of brood years, can be written as:

$$L(S_{i2}, S_{i3}, S_{i4}, M_{i2}M_{i3}|R_i, t_{i2}, t_{i3}, t_{i4}) = \prod_{i=1}^{n}\binom{Ri}{\prod_{j=2}^{4} t_{ij}}(S_{i2}M_{i2})^{t_{i2}} \bullet (S_{i2}S_{i3}M_{i3})^{t_{i3}} \bullet (S_{i2}S_{i3}S_{i4}(1-(M_{i2}+M_{i3})))^{t_{i4}} \bullet$$

$$(1 - S_{i2}M_{i2} + S_{i2}S_{i3}M_{i3} + S_{i2}S_{i3}S_{i4}(1-(M_{i2}+M_{i3})))^{R_i - \sum_{i=2}^{4} t_{ij}} \qquad \text{(EQ 5)}$$

The known constants are the release numbers (R_i), the number of two year olds recovered (t_{i2}), the number of three year olds recovered (t_{i3}), and the number of four year olds recovered (t_{i4}). The expected values of the random variables, t_{i2}, t_{i3}, and t_{i4}, are given in Eq 2, Eq 3 and Eq 4, respectively. The survival probabilities, S_{i2}, S_{i3}, S_{i4} and maturation probabilities, M_{i2}, and $M_{i3,}$ are the parameters to be estimated from the data.

Unfortunately, not all of the parameters are estimable from the data for two reasons. The first being inseparability, meaning that several of the parameters always appear in conjunction with another parameter. The second reason is that there are five parameters and only three minimum sufficient statistics for a release group (Casella and Berger, 1990). Re-parametrization of the model solved the first problem of inseparability and reduced the number of estimated parameters to four. The problem of not enough minimally sufficient statistics was solved when the environmental covariate were introduced into the model.

In order to isolate second year survival in the model, third and fourth year survival and maturation rates were re-parametrized. The term $S_{i3}M_{i3}$ was combined into the parameter θ_1 and the term $S_{i3}S_{i4}(1 - (M_{i2} + M_{i3}))$ was combined into θ_2. The resulting likelihood equation can then be written as

$$L(S_{i2}, M_2, \theta_1, \theta_2 | R_i, t_{i2}, t_{i3}, t_{i4}) = \prod_{i=1}^{n} \binom{R_i}{\prod_{j=2}^{4} t_{ij}} (S_{i2}M_2)^{t_{i2}} \bullet (S_{i2}\theta_1)^{t_{i3}}$$

$$(S_{i2}\theta_2)^{t_{i4}} \bullet (1 - S_{i2}M_2 + S_{i2}\theta_1 + S_{i2}\theta_2)^{R_i - \sum_{i=2}^{4} t_{ij}} \quad . \qquad \text{(EQ 6)}$$

The biological interpretation of the parameter θ_1 is now the probability of surviving and maturing at age 3, given survival to age 2, and the interpretation of θ_2 is the probability of surviving and maturing at age 4, given survival to age 3. S_{i2} and M_{i2} remained unchanged. The parameters M_2, θ_1, and θ_2 were assumed constant across all brood years for a each hatchery, hence the absence of a brood year subscript.

Relationships between environmental factors and CWT tag return numbers were assessed by modelling the second year survival, S_{i2} as a proportional hazards (PH) model.

The proportional hazards model is written as $S_{i2} = (S_o)^{e^{x'\beta}}$, where S_o is the baseline survival, x_i is an environmental covariate and β_ι is a regression parameter expressing the effect of the covariate survival. A PH model was chosen for both its flexibility and ease of parameter interpretation. The probability of surviving to age two is equivalent to the probability of surviving the first summer at sea. Letting S_{i2} be expressed in terms of the effect of an covariate, and holding the other parameters constant, the PH model is actually expressing the effect of the covariate on first summer ocean survival. Substituting the PH model for age two survival into the likelihood (Eq 6) yields the final form of the likelihood model used in the analysis, where

$$L(S_{i2}, \beta_i, M_2, \theta_1, \theta_2 | R_i, t_{i2}, t_{i3}, t_{i4}, x_i) = \prod_{i=1}^{n} \left(\frac{R_i}{\prod_{j=2}^{4} t_{ij}} \right) (S_o{}^{e^{x'\beta}} M_{i2})^{t_{i2}} \bullet (S_o{}^{e^{x'\beta}} \theta_1)^{t_{i3}} \bullet (S_o{}^{e^{x'\beta}} \theta_2)^{t_{i4}} \bullet (1 - S_o{}^{e^{x'\beta}} (M_{i2} + \theta_1 + \theta_2))^{R_i - \sum_{i=2}^{4} t_{ij}} \quad . \quad \text{(EQ 7)}$$

The PH model is equivalent to $h(t) = h_o(t)\exp(x'\beta)$, where *h(t)* is the hazard function (Lee, 1992). The hazard of mortality, at time *t* is proportional to the baseline hazard $h_o(t)$ through a function of the covariate, $e^{x'\beta}$. The hazard ratio, $\frac{h(t)}{h_o(t)}$ is equivalent to $e^{x'\beta}$, and is obtained by dividing both sides of the PH model by $h_o(t)$. Also called the relative risk, the hazard ratio and is the risk of mortality of an individual with covariate *x* compared to an individual with covariate $x = 0$. The value $e^{(x_1 - x_2)\beta}$ is the relative risk of mortality of a population with covariate x_1 relative to a population with covariate x_2. Within this framework, interpretation of the regression parameter, β, becomes easier. For positive values of β, there is an increased risk of mortality for increased values of the covariate x_i. Negative values of the regression parameter indicate a decrease risk of mortality for an increase in the value of the covariate.

The main assumption of the PH model is that the ratio of hazard functions with the same covariate is constant over time. The assumption implies that the biological response to an environmental covariate is constant over time, for an individual and individuals within a species. In other words, an individual salmon from one brood year to the next will have the same biological response to a covariate, and the response by an individual to a covariate does not change over time.

The complexity of the PH models, defined here by the number of covariates in the model, was governed by the number of years of data from the hatcheries. A model with one covariate required the estimation of five parameters, and needed at the very minimum, five degrees of freedom, or five brood years for a hatchery. Since it is not good statistical practice to use all available degrees of freedom in estimation, hatcheries with fewer than seven years of data were not used in the analysis. Conversely, because no hatchery had more than 17 years of data, and most had between 8 and 13 years of data, to be conservative only univariate and bivariate models PH models were analyzed.

Univariate and quadratic models, consisting of only one covariate, were fit first, for each of the nine ocean and environmental conditions defined in Section 2. Models with two covariates were fitted also, using the two best fitting covariates from among the nine univariate models and paired with the other covariates. Due to a lack of consistency in the number of years of data from the hatcheries, no interactions between covariates were analyzed.

The model parameters, S_o, β_i, M_2, θ_1, and θ_2 were estimated using maximum likelihood methods. From the likelihood equation (Eq 7), it is easily shown by factorization that there are six minimum sufficient statistics for the five parameters. The minimum sufficient statistics are $t_{i2}e^{x_i}$, $t_{i3}e^{x_i}$, $t_{i4}e^{x_i}$, t_{i2}, t_{i3} and t_{i4}. A greater number of minimum sufficient statistics than parameters requires iterative methods to solve for the MLE's. Numerical optimization was performed using a program written in the "C" programming language. The log of the likelihood function was entered into the program, and the maximum of the log likelihood was found by iteratively solving for the model parameters. Program output included parameter estimates and variances of the estimates (Fletcher, 1970).

The parameters S_o, M_2, θ_ι, and θ_2 are probabilities with estimates only valid on the interval from 0 to 1. To constrain the parameter estimates on the (0,1) interval, and avoid singularities, it was necessary to reparameteized S_o, M_2, θ_ι, and θ_2. The logit function was used, given by,

$$Parameter = \frac{e^x}{1 + e^x}. \tag{EQ 8}$$

The optimization program could then search the real number space for *x*, and avoid boundary values of 0 or 1. Although probabilities were re-parameterized, the regression parameter (β) was not, and was allowed to take any real value to reflect the effect of the covariate on survival.

Ideally the likelihood function should be a smooth convex function, with parameter estimates maximizing the likelihood. However, given the complex nature of the model, and the variability of the data, the exact behavior of the model was difficult to determine. For most models, (hatchery/covariate combination), the parameter estimates did optimize the likelihood function, and were "well behaved". Good initial seed values for the estimates aided in having the model converge. In the cases where the estimates did not optimize the model, two criteria were used to determine valid estimates. One of the criteria was consistency among estimates of the same parameter for a given hatchery. Recall that the sufficient statistics, t_{i2} t_{i3}, and t_{i4} did not change from one covariate to another, and M_2, θ_1, and θ_2 were held constant across brood years for a hatchery, and so should have approximately the same estimate for all covariates. Therefore, likelihood function values and parameter estimates were determined to be valid based on the consistency of M_2, θ_1, and θ_2 estimates. Initial seed values were chosen on the basis of salmon biology. For example, both the number of jacks (early maturation) and the number of four year-olds tend to be relatively small, therefore low probability values (on the order of 0.05 to 0.15) were chosen as initial seed estimates for M_2 and θ_2.

The regression parameter, β, which was the parameter of interest, assessed the effect of the covariate on smolt survival in the first six months of ocean residence. Hypotheses concerning environmental effects were tested on the basis of the significance of the regression parameters. The hypothesis of interest was H_o: $\beta = 0$ versus H_a: $\beta \neq 0$, and was tested at a significance level of $\alpha = 0.10$. Although the literature suggested a specific direction for the effect of some of the covariates, I was only interested in detecting if an effect was present and used a two-tailed test of significance. Covariates for each model were tested using a z-statistic of the form

$$Z = \frac{\hat{\bar{\beta}}}{\sqrt{\hat{Var}(\hat{\bar{\beta}})}}, \qquad \text{(EQ 9)}$$

under the assumption the MLE is asymptotically normally distributed.

Interannual variability in the CWT returns was high, so there was reason to believe that the variances yielded from the data were under-estimated. The variances obtained directly from the likelihood (Eq 7) are based only on the multinomial sampling error and do not take into account extra likelihood variation resulting from changes in parameter values over time. Because the variances underestimate the true variability and would make the null hypothesis easier to reject, the probability of Type I error is increased. Therefore, the estimated variances were multiplied by a scale parameter to account for some of the year to year variability not explained by the covariate.

The scale parameter was derived from the observed and expected values of the CWT return numbers. The following chi-square formula was used for each model,

$$\chi^2_{df} = \sum_{i=1}^{n}\left(\sum_{j=i}^{4}\frac{(Observed_{ij} - Expected_{ij})^2}{Expected_{ij}}\right) \qquad \text{(EQ 10)}$$

$$df = 3 \bullet n - p \qquad \text{(EQ 11)}$$

where *j* is a cell from the multinomial likelihood, *n* is the number of brood years, *p* is the number of parameters estimated in the model, and *df* are the degrees of freedom. The degrees of freedom for the chi-square was equal to the number of cells multiplied by the number years of data minus the number of estimated parameters (*p*) from the data (Eq 7).

The scale parameter was equal to the chi-square value divided by its degrees of freedom. In all cases the model was overdispersed as indicated by scale parameters greater than 1. The adjusted variance was the estimated variance times the scale parameter. All hypotheses were tested using the adjusted variances, for each of the $\hat{\beta}_{i\iota}$ estimates.

A major problem in assessing the effect of a covariate was inconsistency in regression parameter values and direction (positive or negative) across hatcheries for a specific covariate. For example, the effect of the Pacific Northwest Index (PNI) in the univariate case was significantly positive for three hatcheries, and significantly negative for four hatcheries in the Lower Columbia region. Even more perplexing, for two adjacent hatcheries located in close proximity, the PNI was significantly positive at one and significantly negative at the other. Alternatively, there were covariates for which the regression estimates for all but two of the hatcheries were of the same sign. The question then arose of how to assess which of the covariates really had effects across replicate hatcheries.

To determine if a covariate has an impact on survival, and if so in which direction, consistency among the hatcheries was used as a criteria. To assess consistency of an effect across hatcheries, the mean $\overline{\beta_i}$ for a covariate was estimated, and a t-test using the empirical variance among hatchery values of $\hat{\beta}_i$ was used to test the hypothesis H_o: $\bar{\beta} = 0$ versus H_a: $\bar{\beta} \neq 0$, at a significance level of $\alpha = 0.10$. Since regression coefficients among hatcheries had different variances, a weighted mean was calculated using the following formula,

$$\bar{\beta} = (X'WX)^{-1}X'W\underset{\sim}{\beta} \qquad \text{(EQ 12)}$$

where X is a vector of ones of length equal to the number of regression coefficients, W is a diagonal matrix of weights equal to the inverse of the variance of the coefficients, and $\underset{\sim}{\beta}$ is the vector of the regression coefficients. An average value for a coefficient was calculated both across all hatcheries and by region to look at regional differences in the effect of an environmental factor.

The variance estimate of $\bar{\beta}$ is given by the formula

$$\hat{Var}(\hat{\bar{\beta}}) = \frac{\sum_{i=1}^{n} \frac{W_i(\hat{\beta}_i - \hat{\bar{\beta}})^2}{n-1}}{n \bullet \sum_{i=1}^{n} W_i} . \quad \text{(EQ 13)}$$

The t-test formula to test the hypothesis is

$$t_{df} = \frac{\hat{\bar{\beta}} - 0}{\sqrt{\hat{Var}(\hat{\bar{\beta}})}} , \quad \text{(EQ 14)}$$

where *df* is the degrees of freedom equal to *n-1*. A significant t-test result was interpreted to mean that the effect of a covariate was consistent across all hatcheries. A significant result inferred that the covariate did have an effect on survival to age two.

Coefficients of determination, r^2 values, were not calculated for several reasons. First the non-linear nature of the model does not lend itself to the estimation of r^2 values. Second, the value r^2 measures the amount of variation for single response variable *y* that is explained by the fitted model (Casella and Berger, 1990). However, the CWT data is multivariate, with three response variables rather than one being used to model survival to age two. Moreover, models from a single hatchery are not of interest in this analysis. Determination of the effect of a covariate will be determined by looking at the covariate relationship with survival across all hatcheries.

Non-linear relationships between a covariate and age two survival were evaluated by adding a quadratic term the proportional hazards model. Weighted t-test were also used to look at the significance of the quadratic terms both by region and across all hatcheries. Alternatively, the significance of the quadratic model for each hatchery was also determined through a chi-square statistic with two degrees of freedom, given by

$$\chi_2^2 = \left(\frac{\hat{\beta}_1}{se(\hat{\beta}_1)}\right)^2 + \left(\frac{\hat{\beta}_2}{se(\hat{\beta}_2)}\right)^2 \quad \text{(EQ 15)}$$

where $\hat{\beta}_1$ is the linear coefficient and $\hat{\beta}_2$ is the quadratic coefficient, and the adjusted standard errors are in the denominators. Both methods were used in the analysis.

Results

Data Plots and Relationships

Analysis of the CWT release and return data started with plots of the raw recovery data versus the environmental covariates. Percent returns for each brood year within a hatchery were calculated using the total number of CWT recoveries from all sources and age classes for a brood year divided by the release size of the brood year. Total returns over releases (percent returns) provided a way of looking at the relationships between a rough estimate of survival and the covariates. Although the plots do not represent the relationship between two year old survival and a covariate exactly, logically there should be a component of two year old survival in the total returns.

The data from each hatchery were plotted by region, and only the coastal and lower Columbia regions are represented in the plots. The two Strait of Juan de Fuca hatcheries tended to contradict each other in terms of the direction of an effect and thus there was little to infer from these plots. Each of the lines in Figure 3 represent a different hatchery from the region. All lines were smoothed using a local regression smoother (Chambers and Hastie, 1993). The objective of the raw data plots is to find common trends among the hatcheries of a region, rather than focus on the lines of individual hatcheries. The data used in the plots of percent returns are in Appendix B.

The plots in Figure 3 show the relationship of percent returns versus June monthly and summer average temperature for both the coastal and lower Columbia regions. The strongest trend in the data appears to be in Figure 3b and 3d, which show an increase in returns with an increase in temperature for most of the hatcheries. June temperature appears to have more of a quadratic effect on percent returns (Figure 3a and 3c), with the Lower Columbia hatcheries exhibiting this effect more sharply than the Coastal hatcheries.

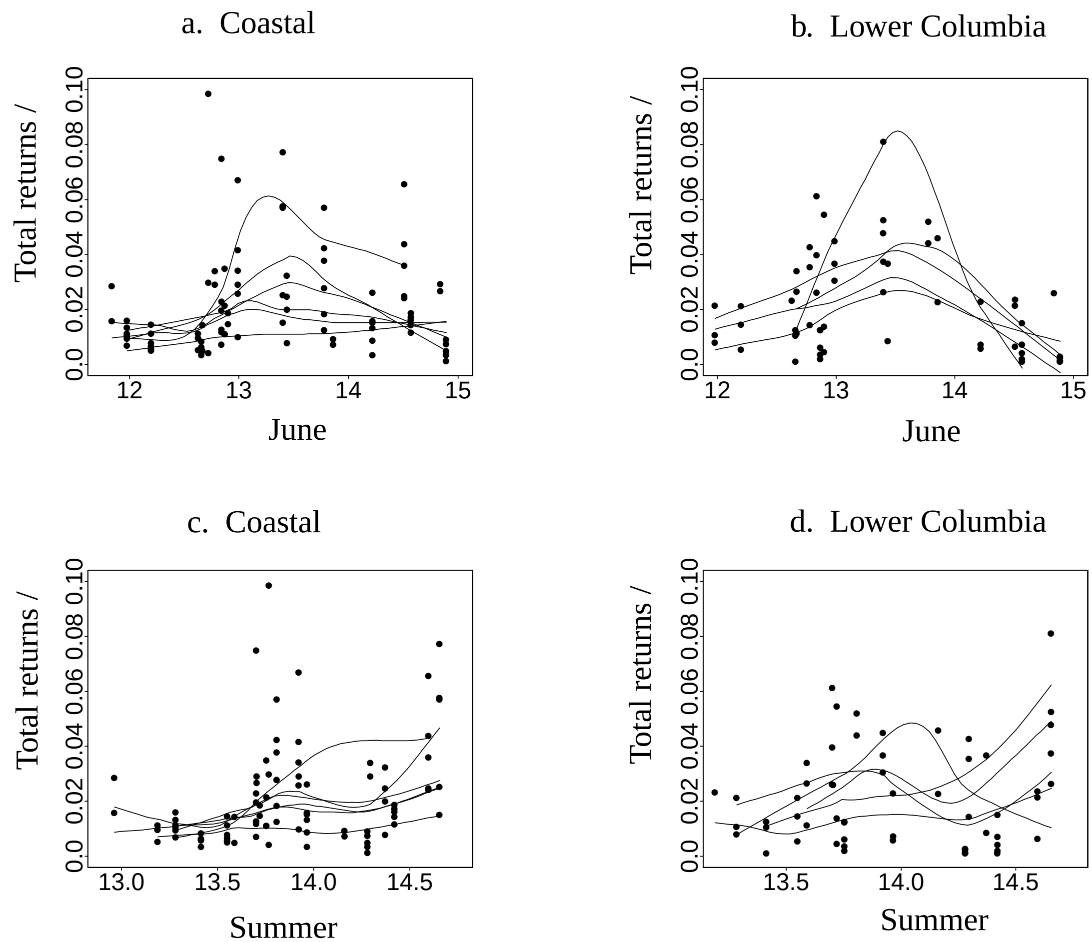

FIGURE 3. Raw data plots of the total number of returns over the number of releases (per brood year) versus sea surface temperature (SST) for June (a and b), and the average for summer months (May - September) (c and d). Each line represents a different hatchery in the Coastal (a and c) and Lower Columbia (b and d) regions.

The two yearly measures of climate condition, the North Pacific Index (NPI) and Pacific Northwest Index (PNI), and their relationship with percent returns are shown in Figure 4. No clear trend between percent returns and the NPI is apparent in Figure 4a and 4b, as indicated by the mostly flat lines in the plots. Only one hatchery in each of the

Coastal and Lower Columbia regions shows a relationship between percent returns and NPI. However, if a relationship were to exist it would most likely be seen in more than one hatchery within a region. Similarly, no consistent pattern of the effect of the PNI on percent returns emerges among the hatcheries in either the Coastal and Lower Columbia regions (Figure 4a or 4b), and therefore a relationship between PNI and percent returns does not seem to be present.

The effect of upwelling conditions at 45^{o} North latitude on percent returns are plotted in Figure 5. The general trend in all plots shows a decrease in percent returns with an increase in the average summer upwelling strength for the two regions (Figure 5b and 5d). The relationship between the average upwelling strength in June and percent returns is less apparent (Figure 5a and 5c), with an initial decrease in survival from 0 to about 50 upwelling units followed by a slight increase in percent returns with increasing upwelling strength. There appears to be some consensus among the hatcheries of a region and between the regions as to the direction of the effects. All plots seem to show decreasing return rates with increasing upwelling strength, although this may be an artifact of a fewer number of data points at the higher values.

The relationships between upwelling conditions at 48^{o} North latitude and percent returns (Figure 6) is more ambiguous than the relationship for 45^{o} North latitude (Figure 5). The plot of summer average upwelling strength at 48^{o} North versus percent returns for coastal hatcheries (Figure 6b) show the greatest agreement among the hatcheries, exhibiting a consistent curvilinear relationship. The nature of the relationship between June upwelling at 48^{o} N and percent returns is more difficult to determine in both the Coastal and Lower Columbia River regions (Figure 6a and 6b), as well as for summer upwelling in Lower Columbia River hatcheries (Figure 6d).

A strong trend between the northern most occurrence of upwelling in June and percent returns is apparent from the plots in Figure 7. Both regions show a general decrease in survival as upwelling conditions extend further north along the coast in the month of June. The trend is more apparent for the hatcheries in the Lower Columbia region than on the coast.

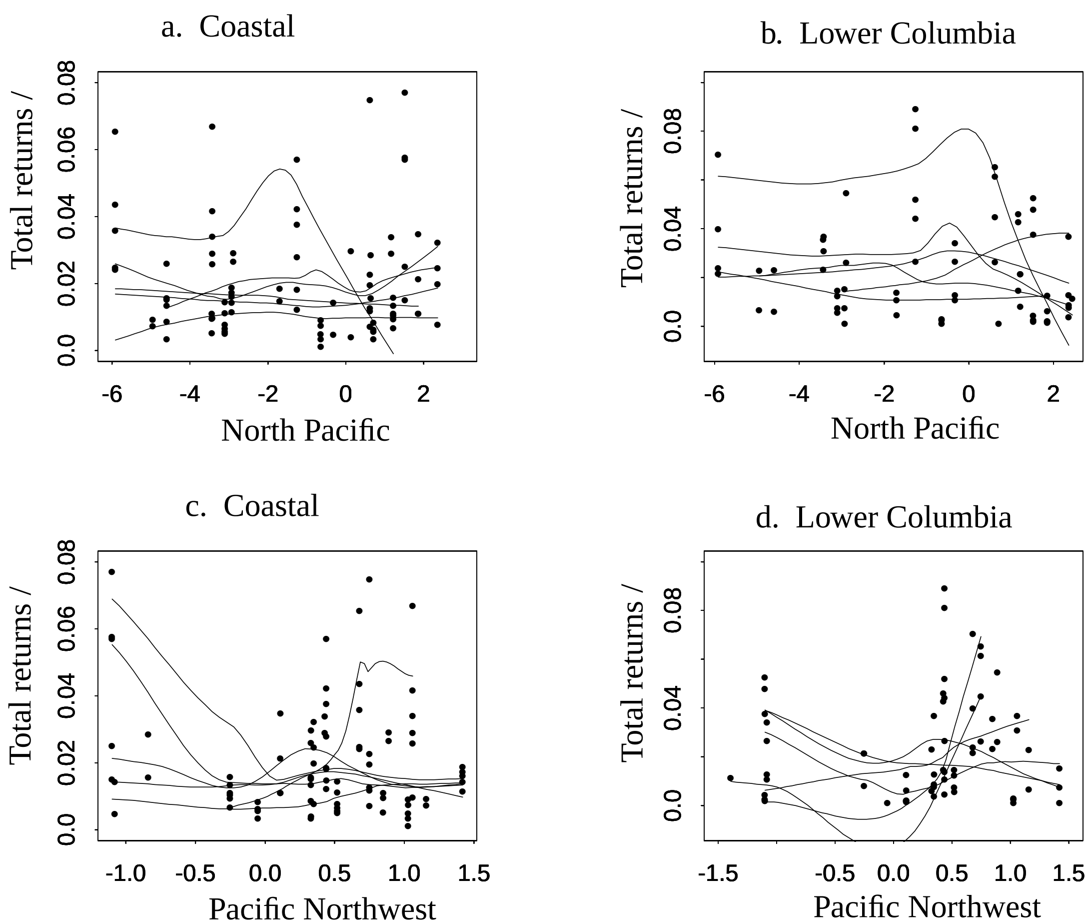

FIGURE 4. Raw data plots of the two yearly climate indices versus the total number of returns over release size (per brood year). The North Pacific Index appears in the first row of plots (a send b) and the Pacific Northwest Index is in the lower row (c and d). Hatcheries for both the Coastal and Lower Columbia regions are shown, with each line representing a different hatchery.

The cumulative upwelling indices at 45^{o} and 48^{o} North are plotted against percent returns in Figure 8. The plots in Figure 8b shows a curvilinear trend with the cumulative index at 45^{o}N among most of the Lower Columbia River hatcheries, and no clear consis-

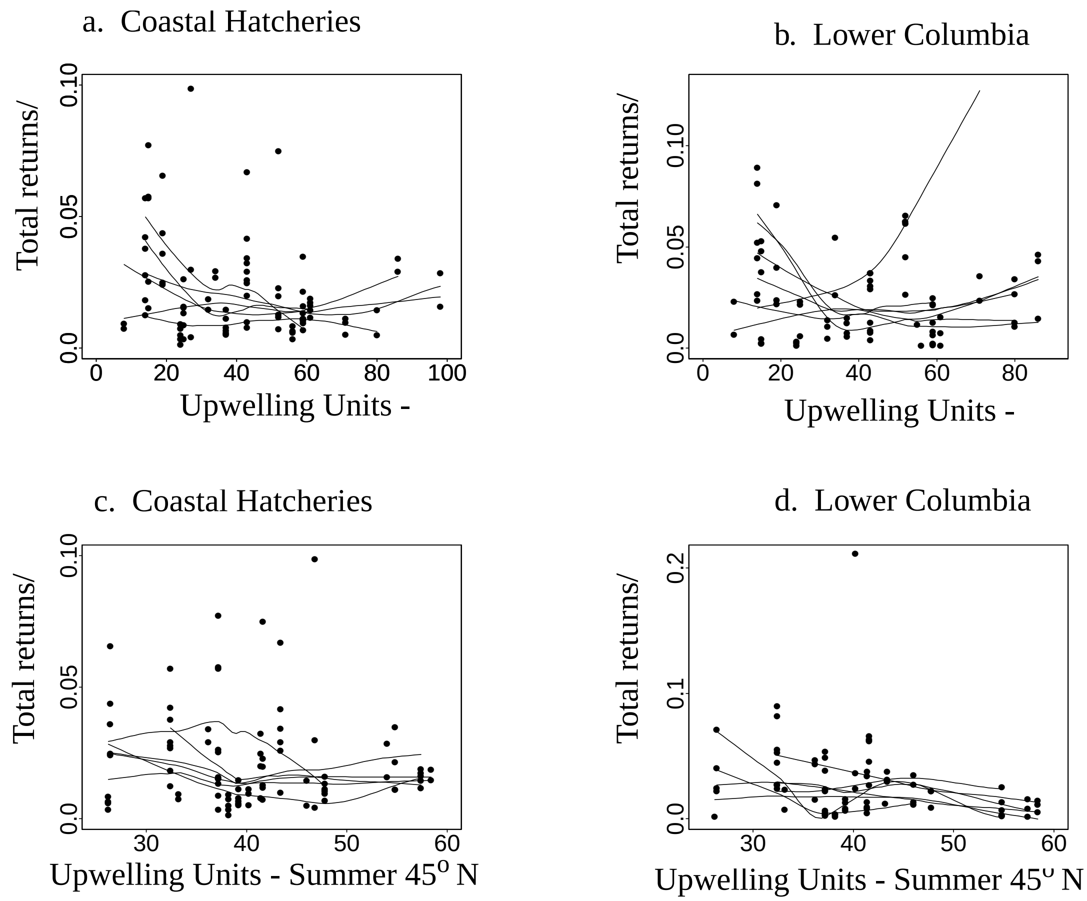

FIGURE 5. Raw data plots of total returns over release size (percent returns) versus upwelling conditions for June and summer (May to September) average at 45° North for hatcheries in the Coastal (a and b) and Lower Columbia River (c and d) regions. Each line represents a different hatchery in the Coastal (a and c) and Lower Columbia (b and d)

tent trend among the hatcheries in the Coastal region (Figure 8a). Both the Coastal and Lower Columbia River plots of percent returns versus cumulative upwelling at 48° N (Figure 8c and 8d), show either a curvilinear, or increasing trend among most of the hatcheries across both regions.

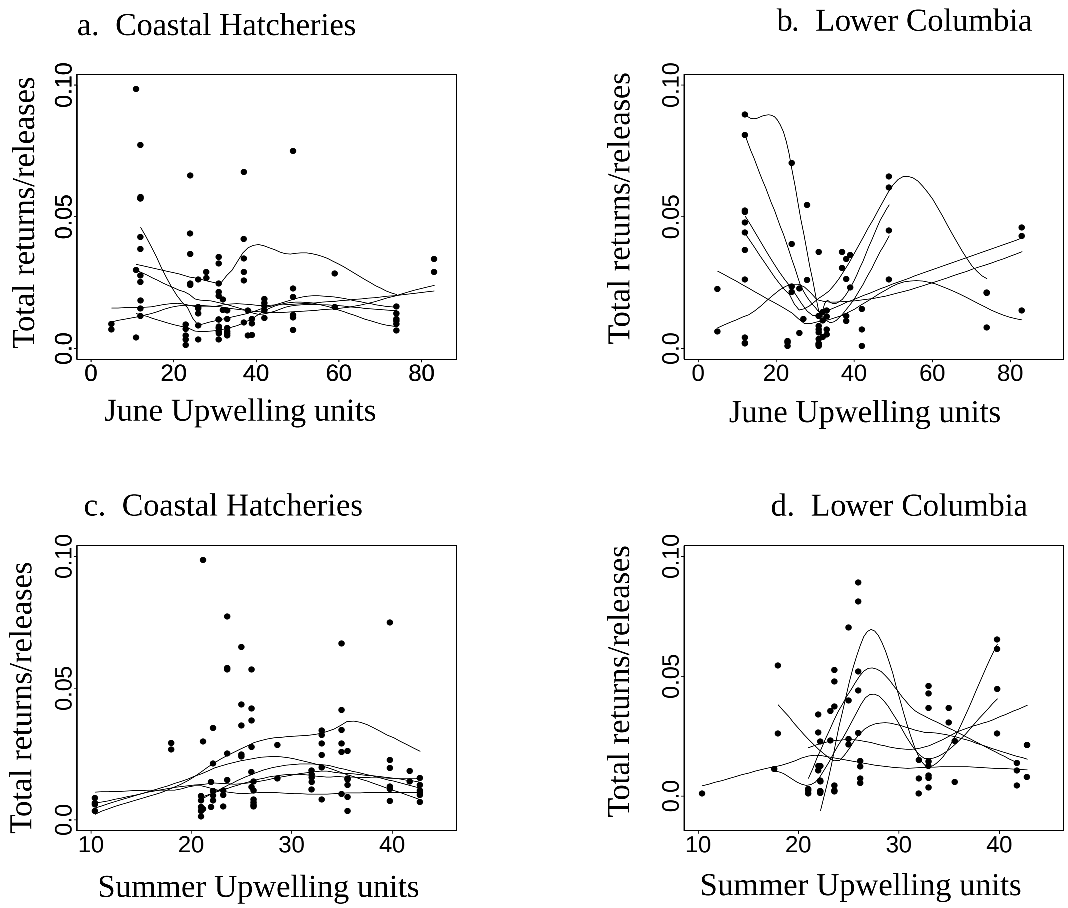

FIGURE 6. Raw data plots of total returns over release size (percent returns) versus upwelling conditions for June and summer (May - September) average at 48^{o} North for hatcheries in the Coastal (a and b) and Lower Columbia (c and d) regions. Each line represents a different hatchery in the Coastal (a and c) and Lower Columbia (b and d) regions.

Several of the covariates are correlated either because they are different measures of the same ocean conditions, or are related through climatically mechanisms (such as North Pacific Index and upwelling conditions). The correlation between covariates was calculated by,

$$corr(x, y) = \frac{\hat{Cov}(x, y)}{\sqrt{\hat{Var}(x)} \bullet \sqrt{\hat{Var}(y)}} , \qquad \text{(EQ 16)}$$

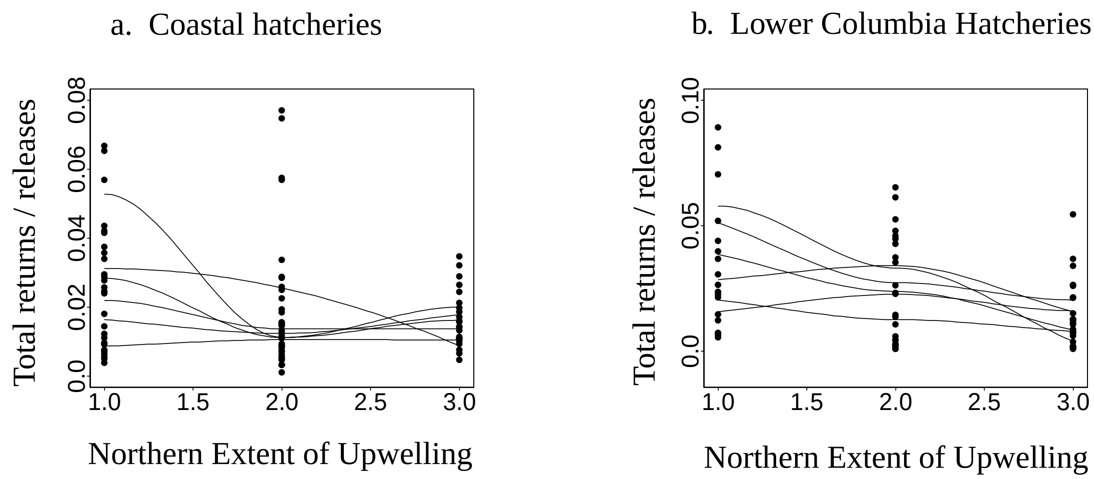

FIGURE 7. Raw data plot of total returns over releases (percent returns) versus Northern extent of June upwelling conditions for hatcheries in the Coastal and Lower Columbia regions. Each line represents a different hatchery in the Coastal (a) and Lower Columbia (b) Rriver regions.

where) $\hat{Cov}(x, y)$ is the empirical covariance between two covariates, and $\hat{Var}(x)$ and $\hat{Var}(y)$ are the empirical variance of each of the covariates. The correlation values are given in Table 2.

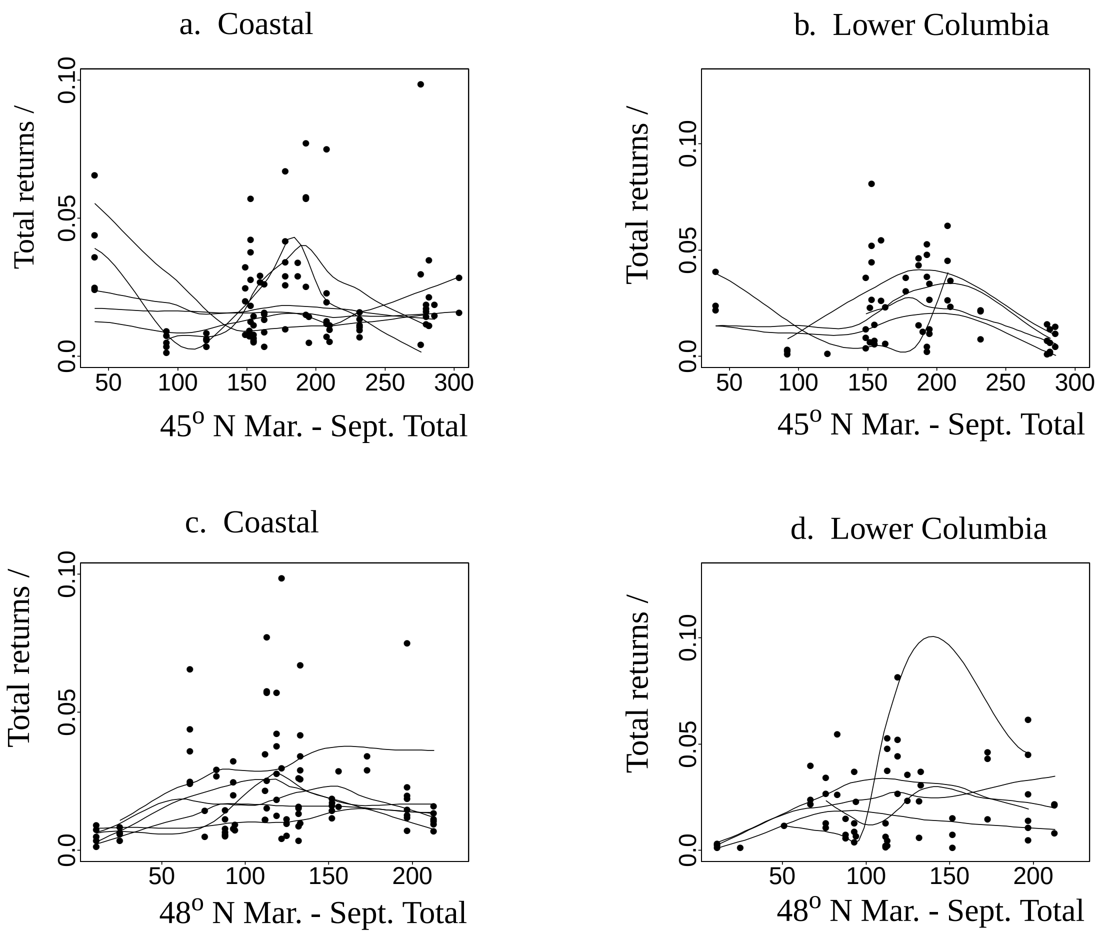

FIGURE 8. Raw data plots of cumulative upwelling indices for the period from March - September versus total return over releases. Each line in a plot represents a different hatchery. Plot a shows no apparent trend, while plot b shows only some of the hatcheries to have a similar curve, but no clear treason. The strongest trends appear in plots c and d, and the model was run for the data in these plots.

TABLE 2. The correlation matrix (n = 22) for the environmental covariates used in the coho survival analysis.

Covariate	**June SST**	**Summer SST**	**NPI**	**PNI**	**June Upwelling 45 N**	**Summer Upwelling 45 N**
June SST	1.000					
Summer SST	0.6061	1.0000				
NPI	-0.4586	-0.2664	1.0000			
PNI	0.4792	0.4375	-0.6179	1.0000		
June 45 N Upwelling	-0.5761	-0.4943	0.4104	-0.3263	1.0000	
Summer 45N Upwelling	-0.3522	-0.2461	0.2902	-0.1350	0.4268	1.0000
June 48N Upwelling	-0.4818	-0.2541	0.3027	-0.0949	0.7906	0.3009
Summer 48N Upwelling	-0.1911	0.1351	-0.0375	0.2010	0.0937	0.4466
Northern Upwelling Extent	0.0121	-0.2101	0.5104	-0.3446	0.4865	0.3995
Cumulative Upwelling 45 N	-0.4964	-0.3652	0.3531	-0.2073	0.4494	0.8771
Cumulative Upwelling 48 N	-0.4022	-0.0641	0.0716	0.0872	0.2898	0.5102

TABLE 2. (continued)

Covariate	June Upwelling 48 N	Summer Upwelling 48N	Northern Upwelling Extent	Cumulative Upwelling 45 N	Cumulative Upwelling 48 N
June 48N Upwelling	1.0000				
Summer 48N Upwelling	0.5046	1.0000			
Northern Upwelling Extent	0.3641	0.0340	1.0000		
Cumulative Upwelling 45 N	0.2736	0.2961	0.3123	1.0000	
Cumulative Upwelling 48 N	0.5754	0.8454	0.0476	0.6175	1.0000

Regression Relationships - Univariate

Results of the univariate analysis showed three of the nine climate/ocean condition covariates to be significant. One of the three was a measure of temperature and the other two were different measures of upwelling conditions and therefore correlated. Table 3 provides a summary of the univariate analyses for the nine covariates. The mean of the regression coefficient, its standard error and its associated p-value are given both by region and across all hatcheries. The summary gives some idea as to the variability of the results. The significance of a covariate was based on the results of the weighted t-test of H_o: $\bar{\beta} = 0$, versus Ha: $\bar{\beta} \neq 0$, where $\bar{\beta}$ is the weighted mean of the regression parameter across all hatcheries. Results from individual hatcheries are given in Appendix C.

TABLE 3. A Table showing the results of the univariate analysis by region and across all hatcheries (overall average). The regression coefficient is the weighted mean across all hatcheries. Also given are the standard error of the weighted mean, the p-value of the weighted t-test and a 90% Confidence Interval for the mean. Shaded areas denote significance at the α = 0.10 level

	Region (number of hatcheries)			
Covariate	**Strait (2)**	**Coastal (6)**	**Lower Columbia (7)**	**Overall Average (15)**
June SST				
$\hat{\bar{\beta}}$	-0.0191	-0.0180	0.1324	0.0982
$\hat{SE}(\hat{\bar{\beta}})$	0.090	0.0062	0.0599	0.0730
p-value	0.956	0.077	0.069	0.20
90% C.I.	(-0.5873, 0.5491)	(-0.0305, -0.0055)	(0.0161, 0.2487)	(-0.0268, 0.2223)
Summer SST				
$\hat{\bar{\beta}}$	0.0194	-0.1796	-0.0188	-0.0992
$\hat{SE}(\hat{\bar{\beta}})$	0.279	0.0102	0.0270	0.0422
p-value	0.956	<0.001	0.513	0.034
90% C.I.	(-1.742, 1.781)	(-0.2000, -0.1591)	(-0.0713, 0.0337)	(-0.1735, -0.0249)
North Pacific Index				
$\hat{\bar{\beta}}$	0.0465	-0.0083	-0.0086	0.0032
$\hat{SE}(\hat{\bar{\beta}})$	0.0052	0.0015	0.0146	0.0125
p-value	0.071	0.003	0.576	0.805
90% C.I.	(0.0138, 0.0791)	(-0.0113, -0.0053)	(-0.0369, 0.0197)	(-0.0189, 0.0252)
Pacific Northwest Index				
$\hat{\bar{\beta}}$	-0.0904	0.0839	0.0077	0.0305
$\hat{SE}(\hat{\bar{\beta}})$	0.0108	0.0739	0.0257	0.0428
p-value	0.075	0.308	0.774	0.488
90% C.I.	(-0.1584, -0.0224)	(-0.065, 0.2328)	(-0.0423, 0.0577)	(-0.0449, 0.1059)

TABLE 3. A Table showing the results of the univariate analysis by region and across all hatcheries (overall average). The regression coefficient is the weighted mean across all hatcheries. Also given are the standard error of the weighted mean, the p-value of the weighted t-test and a 90% Confidence Interval for the mean. Shaded areas denote significance at the α = 0.10 level (Continued)

	Region (number of hatcheries)			
Covariate	**Strait (2)**	**Coastal (6)**	**Lower Columbia (7)**	**Overall Average (15)**
45^o N June Upwelling				
$\hat{\bar{\beta}}$	-0.0003	0.0020	0.0005	0.0010
$\hat{SE}(\hat{\bar{\beta}})$	3.1 x 10^{-8}	0.0002	0.0015	0.0006
p-value	<0.001	<0.001	0.761	0.088
90% C.I.	(-0.0002871, -0.0002867)	(0.0016, 0.0024)	(-0.0026, 0.0035)	(0.00004, 0.0020)
45^o N Summer Upwelling				
$\hat{\bar{\beta}}$	0.0044	4.98 x 10^{-6}	0.0019	3.0 X 10^{-5}
$\hat{SE}(\hat{\bar{\beta}})$	0.0003	5.6 x 10^{-5}	0.0057	0.0003
p-value	0.038	0.933	0.749	0.915
90% C.I.	(0.0024, 0.0061)	(0.00011, -0.00012)	(-0.0091, 0.0129)	(-0.0005, 0.0005)
48^o N June Upwelling				
$\hat{\bar{\beta}}$	-0.0002	0.0020	-0.0037	-0.0014
$\hat{SE}(\hat{\bar{\beta}})$	1.5 x 10^{-5}	0.0016	0.0089	0.0042
p-value	0.042	0.280	0.693	0.749
90% C.I.	(-0.0003, -0.0001)	(-0.0013, 0.0052)	(-0.0209, 0.0136)	(-0.0087, 0.0060)
48^o N Summer Upwelling				
$\hat{\bar{\beta}}$	0.0058	0.0004	-0.0034	-7.4 x 10^{-5}
$\hat{SE}(\hat{\bar{\beta}})$	0.0011	0.0030	0.0038	0.0024
p-value	0.115	0.896	0.406	0.976

TABLE 3. A Table showing the results of the univariate analysis by region and across all hatcheries (overall average). The regression coefficient is the weighted mean across all hatcheries. Also given are the standard error of the weighted mean, the p-value of the weighted t-test and a 90% Confidence Interval for the mean. Shaded areas denote significance at the α = 0.10 level (Continued)

	Region (number of hatcheries)			
Covariate	**Strait (2)**	**Coastal (6)**	**Lower Columbia (7)**	**Overall Average (15)**
90% C.I.	(-0.0009, 0.0125)	(-0.0059, 0.0067)	(-0.0111, 0.0042)	(-0.0043, 0.0042)
Northern Extent Upwelling				
$\hat{\bar{\beta}}$	0.0157	0.0312	0.0775	0.0468
$\hat{SE}(\hat{\bar{\beta}})$	0.1292	0.0064	0.0305	0.0174
p-value	0.923	0.005	0.043	0.018
90% C.I.	(-0.8000, 0.8314)	(0.0183, 0.0441)	(0.1871, 0.1363)	(0.0161, 0.0775)
Cumulative Upwelling 45 North				
$\hat{\bar{\beta}}$	-0.0450	-0.0798	-0.3344	-0.0063
$\hat{SE}(\hat{\bar{\beta}})$	0.0146	0.1039	0.0614	0.0177
p-value	0.200	0.477	0.002	0.728
90% C.I.	(-0.1375, 0.04744	(-0.2892, 0.1296)	(-0.4538, -0.2150)	(-0.0375, 0.0249)
Cumulative Upwelling 48 North				
$\hat{\bar{\beta}}$	-0.0450	-0.0798	-0.3344	-0.1318
$\hat{SE}(\hat{\bar{\beta}})$	0.0146	0.1039	0.0614	0.0768
p-value	0.200	0.477	0.002	0.108
90% C.I.	(-0.1375, 0.0474)	(-0.2892, 0,1296)	(-0.4538, -0.2150)	(-0.2672, 0.0035)

Summer average temperature, defined as the average temperature from May through September, was found to have a significant effect on survival (p = 0.034). The overall mean regression coefficient $\hat{\bar{\beta}}$ was -0.0992, indicating an increase in survivorship with an increase in temperature. A regression coefficient of -0.0992 in a proportional hazards model would mean a fish exposed to a 1^{o} C higher average summer temperature has 90.6% the risk of mortality compared to a fish exposed to the lower temperature.

Average summer temperature was also significant among coastal hatcheries ($p < 0.001$). The strong similarly among hatcheries of the Coastal region as to the relationship between summer temperature and survivorship is apparent in Figure 9a. There is less concurrence among the hatcheries of the lower Columbia region as to the effect of summer temperature (Figure 9b), with a mean regression coefficient of -0.0188 ($p = 0.531$). The results of the univariate analysis, and the survivorship curves in Figure 9 are supported by the plots of the raw data in Figure 3b and 3d.

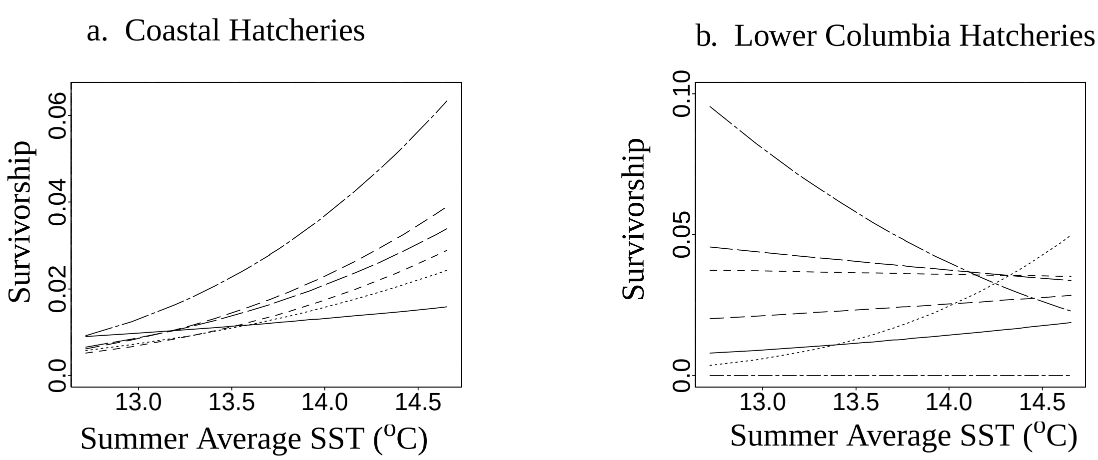

FIGURE 9. Plots of summer (May - September) average sea surface temperature (SST) versus the fitted survivorship curve for hatcheries in the Coastal and Lower Columbia River regions. Each line represents a different hatchery in the Coastal (a) and Lower Columbia River (b) regions.

The strength of coastal upwelling at 45^{o}N in June ($p = 0.088$) and the Northern Extent of coastal upwelling in June ($p = 0.018$) were two significant upwelling condition covariates. The value of the mean regression coefficient for June 45^{o}N upwelling was 0.001, which translates into a 1.001 relative risk of mortality for a smolt exposed to a one unit stronger upwelling condition than a fish exposed to the weaker upwelling condition. Expressed another way, for two fish with the same baseline survival of 0.05, and differing only in one unit of upwelling strength, the smolt exposed to the higher upwelling will have a 0.02% lower survival rate. A plot of June upwelling strength versus survivorship, for hatcheries in both the Coastal and Lower Columbia regions is given in Figure 10. The survivorship curves in Figure 10 agree with overall trends seen in the raw data plots in Figure 5a and 5c, showing a decreasing survival with increasing upwelling strength.

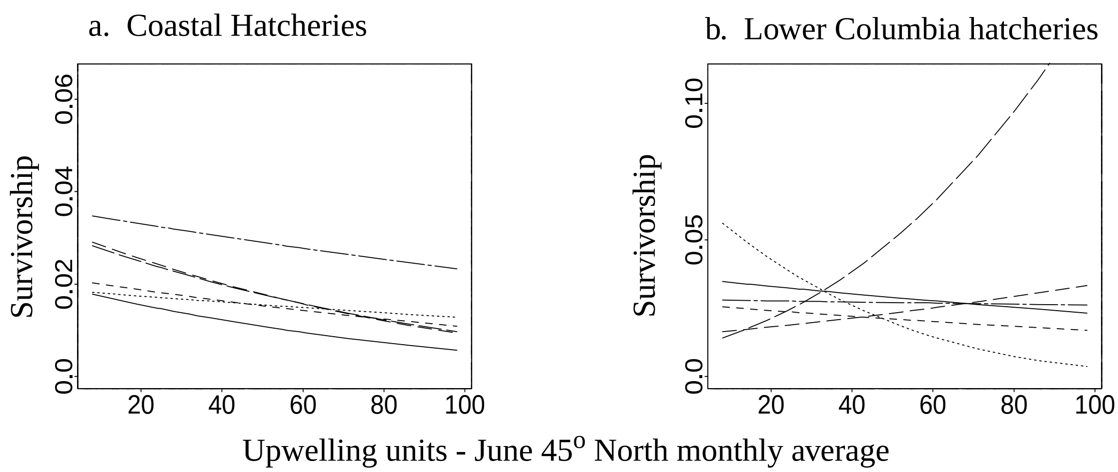

FIGURE 10. Plots of upwelling conditions at 45° North latitude versus fitted survivorship for coastal and lower Columbia river hatcheries. Each line represents a different hatchery in the Coastal (a) and Lower Columbia (b) regions.

Extent of northern upwelling conditions for the month of June was the most significant univariate coefficient with a mean regression coefficient value of 0.0468 ($p = 0.018$). The positive value indicates lower survival in years when coastal upwelling conditions in June moved further to the north. The coefficient value suggests that for two fish, both having a baseline survival of 5% ($S_o = 0.05$), there will be a 0.67% lower survival rate for those fish outmigrating in a year where the upwelling conditions occurred three degrees latitude further north than fish outmigrating in another year. Figure 11 shows plots of northern upwelling extent versus survivorship. For all but two of the hatcheries in Figure 11 there is decreasing survival as June upwelling occurs further north.

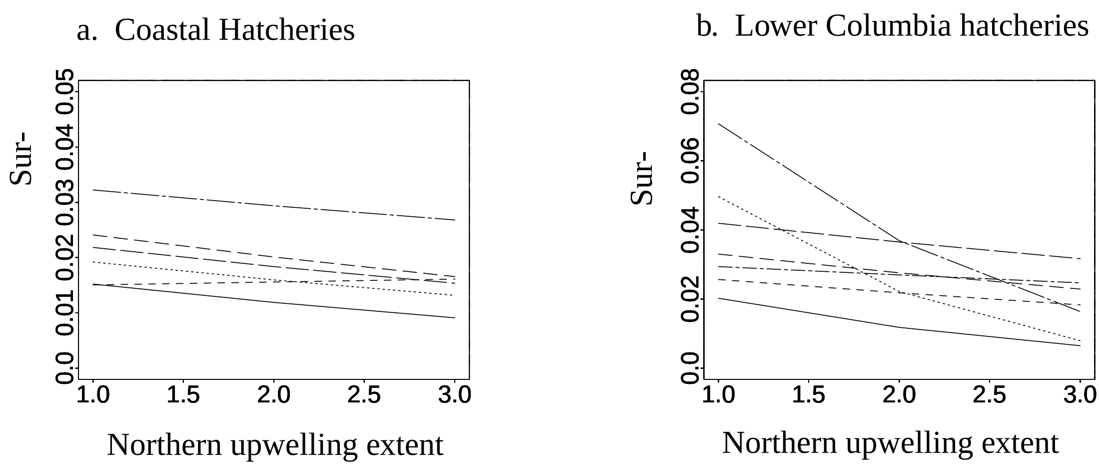

FIGURE 11. Plot showing the relationship between the northern extent of June upwelling versus fitted survivorship for the hatcheries in the Coastal and Lower Columbia regions. Each line represents a different hatchery in the Coastal (a) and Lower Columbia (b) regions.

The cumulative upwelling covariate at 48^o N was marginally non-significant (p = 0.108). However, all hatcheries showed a positive relationship (negative coefficient) between the total upwelling index values from March to September and survival to age two. Overall mean of the coefficient was -0.1318, which implies that for two fish having the same baseline survival of 5% (S_o = 0.05), there will be a 2.2% increase in the survival rate for the fish outmigrating in the year with a one index unit increase the cumulative upwelling. The consistency of effect of the cumulative upwelling covariate across the hatcheries was apparent in the raw data plot (Figure 8) and again emerges in Figure 12. Also apparent in Figure 12 is the degree of the effect of the cumulative upwelling covariate on age two survival, as seen on the sharp slopes of the lines from several of the hatcheries. The marginal significance of this covariate is probably due to the variance of the mean regression coefficient, and the standard errors of the estimates of the coefficients from the hatcheries (see Appendix C, Univariate Model Results).

Neither the Northern Pacific Index, nor the Pacific Northwest index were found to

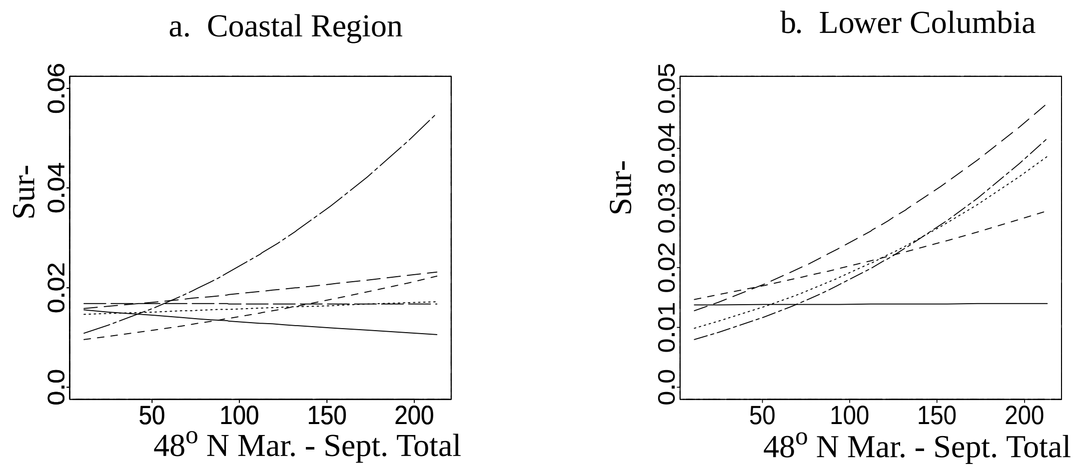

FIGURE 12. Plots of model results from the analysis using cumulative monthly upwelling conditions at 48º N as the covariate. Each line represents a different hatchery in the Coastal (a) and Lower Columbia (b) regions. All but two of the coastal hatcheries show a positive association between upwelling and survivorship (a). In the Lower Columbia region (b), all hatcheries had a positive association between upwelling and the covariate. The line that appears to have a downward slope plot b is from Gray's River Hatchery, which had coefficient value of nearly zero. The line is almost flat, but when plotted on this scale, with the other lines, it appears to have a negative slope.

be significant across all hatcheries (p = 0.805 and p = 0.488, respectively). However, NPI had a significant regional effect on the coast (p = 0.003). Both of these indices are yearly measurements of climate conditions, and as such may not provide enough of a signal during the period from outmigration to jack return (the two-year old survival period, May to November) to be detected in the analysis. Positive and negative values for the regression coefficients were evenly distributed among the hatcheries for both indices. The inconsistency in the direction of an effect lead to the non-significant result. Upwelling conditions as measured at 48º N latitude for June (p = 0.915) and 48º N latitude for both June and Summer averages were also found to be non-significant (p = 0.749 and p = 0.976, respectively), again due to the inconsistency in effects among the hatcheries.

Quadratic Effects

Four of the covariates were fitted to a quadratic polynomial in the proportional hazards (PH) model. The choice of which covariate to model as a quadratic was based on significance of the overall mean of the coefficient and on the plots of the raw data. If a mean regression coefficients across all hatcheries was significant, or if there was a definite curvilinear trend across multiple hatcheries in the raw data plots, then these covariates were modelled as a quadratic polynomial in the PH model. The quadratic term is a way to show non-linearity between a covariate and survival to age two.

The quadratic PH model for survival to age two is given by

$$S_{i2} = (S_o)^{e^{\beta_1 x + \beta_2 x^2}} . \qquad \text{(EQ 17)}$$

In the PH model, a positive coefficient in the quadratic term indicates the vertex is a maximum point, and a negative coefficient indicates the vertex is a minimum. The covariate value at the maximum (or minimum) is given by

$$maximum = -\frac{\beta_1}{2\beta_2} . \qquad \text{(EQ 18)}$$

A significant quadratic term suggests a non-linear model is a better fit for the covariate than a model with a strictly increasing or decreasing relationship with the covariate. As with the univariate model, the significance of a covariate was based on the results of a weighted t-test of the mean of the quadratic term across all hatcheries, testing the hypothesis $H_o: \bar{\beta}_2 = 0$ versus $H_a: \bar{\beta}_2 \neq 0$. Results of the quadratic analysis are summarized in Table 4.

Summer average sea surface temperature (SST) and June upwelling at 45^o N had significant mean regression coefficients with $p = 0.034$ and $p = 0.088$, respectively. Cumulative upwelling at 48^o N was marginally non-significant ($p = 0.108$), however, a curvilinear trend was apparent in the raw data plots of Figure 8. June SST was non-significant, but the plots of June SST versus percent returns showed the strongest evidence of a quadratic effect. Northern upwelling extent was the only significant covariate not modelled as a quadratic because with only three values for this covariate, fitting a 2nd degree polynomial would not have yielded meaningful information. The SST and upwelling condition values had to be standardized in the analysis so that the model would converge more readily.

The significant quadratic coefficients were the two upwelling conditions, June upwelling at 45^{o} N and cumulative upwelling at 48^{o} N. Neither SST covariate had a significant quadratic coefficient, although if the two Strait of Juan de Fuca hatcheries were taken out of the analysis, the June SST quadratic term would be significant ($p = 0.085$), with a value of 0.12562. The quadratic coefficient for summer SST was non-significant ($p = 0.723$), however the linear term was ($p = 0.026$), agreeing with the results of the univariate analysis.

June SST is plotted against survivorship from the quadratic model in Figure 13a and 13b. The survivorship curves show a remarkable similarity with the raw data plots of June SST versus percent returns (Figure 3), and seem to capture the essence of the June temperature/percent return relationship. The two plots of Figure 13 a - b also demonstrate why the overall average across the two regions was significant, with all hatcheries having a similar survivorship curve. The most striking feature of the two plots is the near alignment of the maxima for the hatcheries. The plots of survivorship versus summer SST (Figure 13c and 13d), show a lack of consensus among both the hatcheries and regions as to the effect of summer average SST on survival to age two, and subsequently the reason for the resulting non-significance ($p = 0.723$) of the summer quadratic term.

The resulting PH models for the two upwelling conditions are plotted in Figure 14. The plots for the cumulative upwelling quadratic model show a similar pattern to the June SST plots. Among most of the hatcheries in both the Coastal and Lower Columbia River regions, there is a similar pattern of survival relationships (Figures 13a and 14b) and again the maximum for the hatcheries in the coastal region seems to be in a narrow range of upwelling values. The lines of the plots also resemble the smoothed curves in the raw data plots of Figure 8, suggesting that the relationship between survival and cumulative upwelling is not strictly increasing. The plots for 45^{o} N upwelling are less interesting (Figure 14c and 14d), and although the quadratic term was significant, the lack

TABLE 4. A table showing a summary of the quadratic model results. Significance of a model was measured by the overall mean regression coefficient p-value. Mean regression coefficients for each region are also given in the table. Shaded areas denote significance at the $\alpha = 0.10$ level.

	June SST		**Summer SST**		**June Upwelling 45 North**		**Cumulative Upwelling 48 North**	
Region	**Linear Term $\hat{\beta}_1$**	**Quadratic Term $\hat{\beta}_2$**	**Linear Term $\hat{\beta}_1$**	**Quadratic Term $\hat{\beta}_2$**	**Linear Term $\hat{\beta}_1$**	**Quadratic Term $\hat{\beta}_2$**	**Linear Term $\hat{\beta}_1$**	**Quadratic Term $\hat{\beta}_2$**
Strait of Juan de Fuca								
Coefficient estimate	0.02276	-0.04307	-0.01201	-0.04561	0.00267	-0.03962	-2.6230	0.73830
p - value	0.758	0.006	0.976	0.005	0.909	0.648	<0.001	0.001
Coastal Hatcheries								
Coefficient estimate	-0.04875	0.07331	-0.06368	-0.02817	0.05436	-0.05971	-2.3136	0.61242
p - value	0.014	0.059	0.046	0.191	0.003	<0.001	0.002	0.004
Lower Columbia								
Coefficient estimate	0.01887	0.16184	-0.05089	0.04563	0.04817	-0.05003	-1.3166	0.15574
p - value	0.604	0.242	0.201	0.760	0.193	0.131	0.059	0.295
Overall Average								
Coefficient estimate	-0.00026	0.10085*	-0.05664	-0.01316	0.04189	-0.05449	-1.7053	0.25716
p - value	0.991	0.2534*	0.026	0.723	0.005	<0.001	<0.001	0.051

Note: *For June Temperature, the average of the quadratic term across all hatcheries is the Coastal and Lower Columbia regions was 0.12562

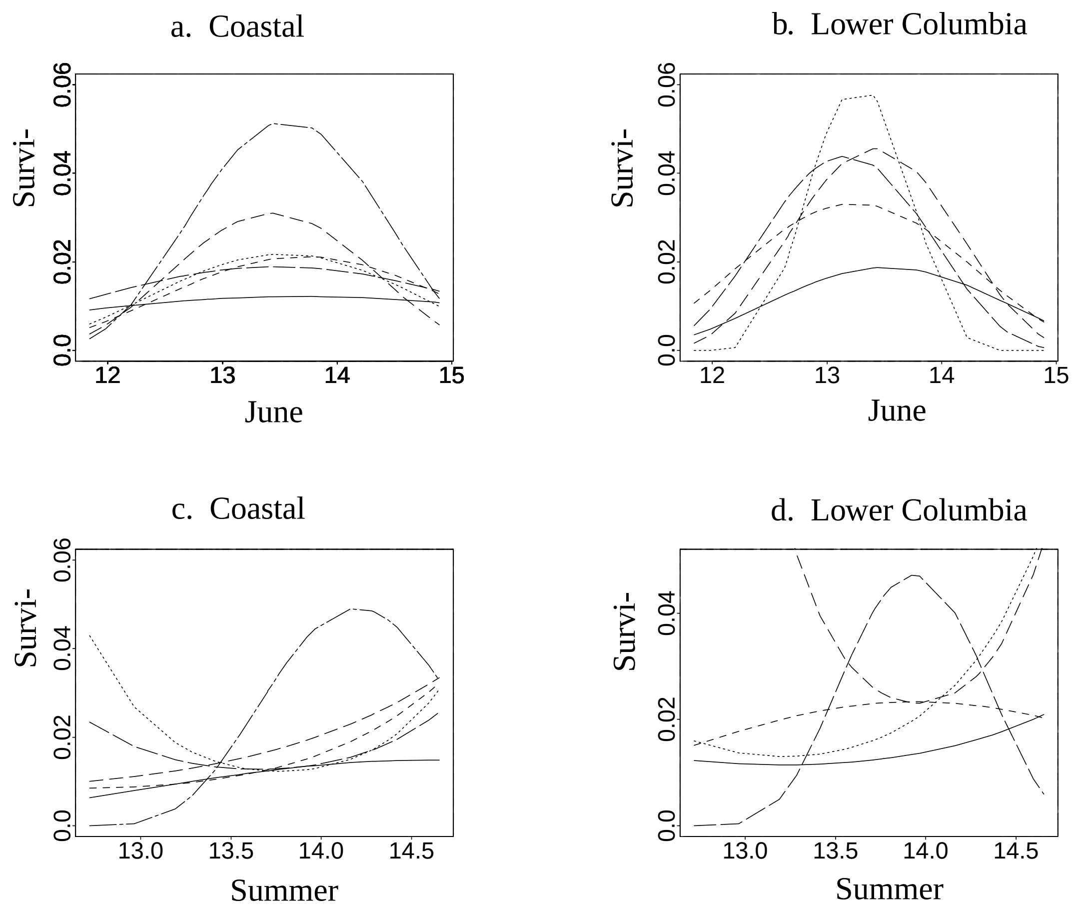

FIGURE 13. Plots of the quadratic relationship between June monthly (a and b) and Summer average (c and d) sea surface temperature (SST) and survivorship. Each line represents a different hatchery in the Coastal (a and c) and Lower Columbia (b and d) regions.

of a clear overall pattern makes the results difficult to interpret.

Using data and parameter estimates from the Quinault NFH, several diagnostic plots were made for the June SST and cumulative upwelling quadratic models. The hatchery was chosen because it had the greatest number of years of data, and the parameter estimates were representative of the overall coefficient averages. The diagnostic plots in Figure 15 are for the June SST and 48^{o} N cumulative upwelling quadratic models. Observed adult returns from all age classes were plotted against total adult returns from all

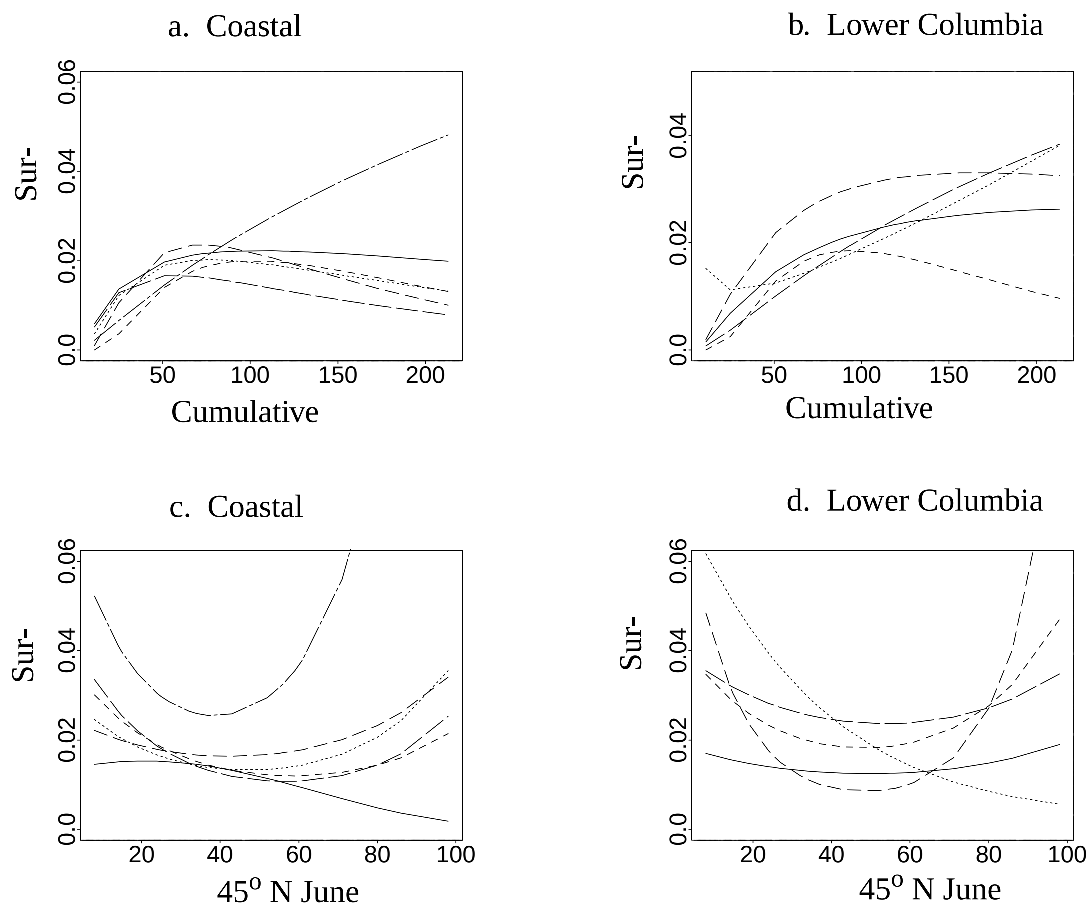

FIGURE 14. Plots of the quadratic upwelling condition models for the Coastal and Lower Columbia River regions. The top row plots (a and b) are for the March - September cumulative upwelling index at 48^{o} N, and the bottom row (c and d) is for the June upwelling strength and 45^{o}N. Each line represents a different hatchery in the Coastal (a and c) and Lower Columbia (b and d) regions.

age classes predicted by the quadratic model (expected values). A model which fits the data well would have the estimates of total adult returns (expected values) close to the observed values, and falling along the 45^{o} line in the plots. The scatter of points about the line in Figure 15a shows a high degree of variability for the June SST model. However, the cumulative upwelling model seems to fit the data well for lower observed values (Figure 15b), with higher variability for increasing observed values.

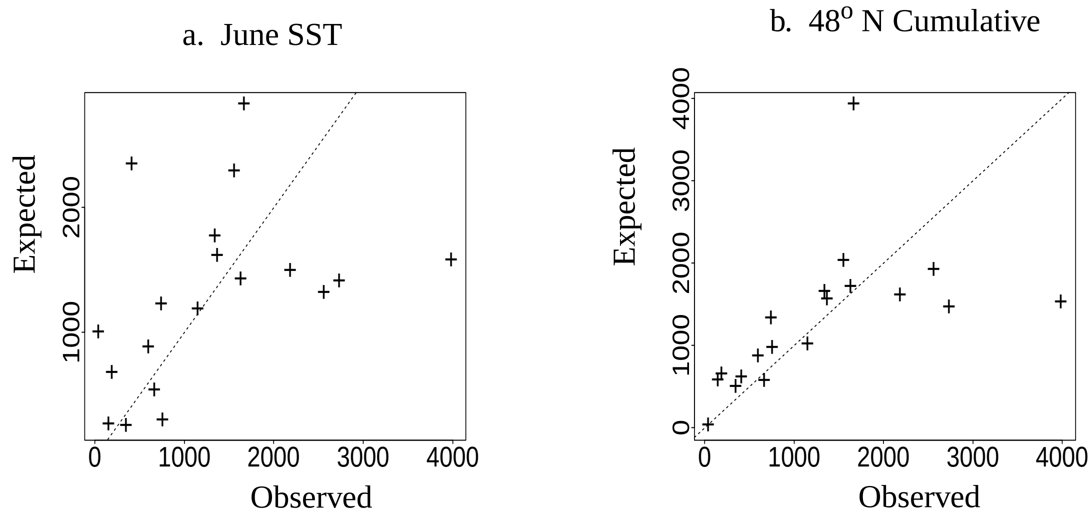

FIGURE 15. Plots of the observed versus expected total adult returns for the June sea surf SST quadratic model and the 48° N cumulative upwelling model. If a model fits the data well, the points should fall along the 45° line, represented by the dotted line. The cumulative upwelling model seems to fit the data better than the June sea surface temperature (SST) model, as indicated by the clustering of points about the 45° line.

Residual values, the difference in the observed and expected values, were plotted against the covariate in Figure 16. The residual diagnostic for both the univariate and quadratic models are shown to illustrate the differences in the models and to assess the effect of the quadratic term on the residuals. Although there does not appear to be a large difference in the residual plots between the univariate and quadratic models for June SST, the addition of the quadratic term reduced the residual deviance from a value of 19,490.78 (squared deviancies 38,087,223) in the univariate model to a value of 12.72 (squared deviancies 17,222,887) in the quadratic model. The quadratic term of cumulative upwelling (Figure 15c and 15d) changed the deviance from -22.28 (squared deviance 17,586,976) to 12.86 (squared deviance 14,825,254). Both the sign change and reduction in value of the residual deviance indicate that the relationship between two year old survival and June SST and 48° cumulative upwelling is quadratic (non-linear) in nature, and that the quadratic model better fits the data.

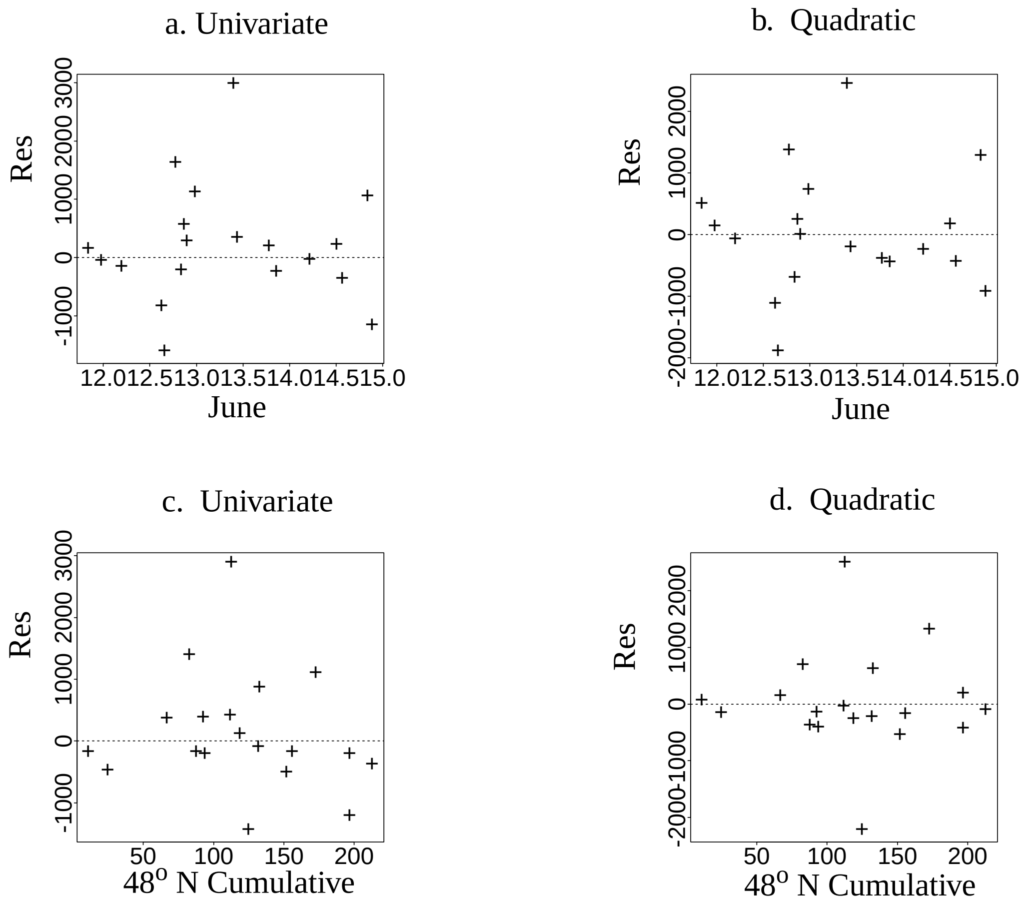

FIGURE 16. Diagnostic residual plots showing the covariate values versus the residual values (observed values minus expected values) for both the univariate (linear) and quadratic models. In both cases, the bivariate models exhibit less bias (points are more evenly distributed above and below the 0 line).

Bivariate Analysis

Choice of which bivariate models to investigate was based on the results of the univariate analysis. The two most significant univariate climate/ocean conditions, summer average temperature and northern upwelling extent were paired with all other covariates. As with the univariate analysis, a significance was determined using a weighted t-test of the regression coefficients from all hatcheries, testing H_o: $\bar{\beta} = 0$, versus Ha: $\bar{\beta} \neq 0$ The results of the bivariate analysis appears in Table 5.

Some of the non-significant covariates in the univariate analysis became significant when paired with another covariate. Summer average temperatures was almost always significant when it appeared in the model with another covariate. June temperature is an example of a covariate that was non-significant in the univariate model, but significant when paired with both summer temperature and northern upwelling extent ($p = 0.060$ with summer temperature and $p = 0.012$ with northern upwelling extent). However, the sign of the estimate of the regression coefficient was different in the two models, with a positive value (negatively correlated with survivorship) when paired with summer and a negative value (positively correlated with survivorship) when paired with northern upwelling extent. Upwelling strength at 45^o North for June was significant ($p = 0.003$) only when paired with summer temperature, as were 45^o North summer upwelling and 48^o North June upwelling strength. Cumulative upwelling at 48^o N was significant ($p = 0.064$) only with summer SST and cumulative upwelling at 45^o N was significant when paired with Northern upwelling extent ($p = 0.095$). Northern extent of upwelling was only significant when paired with a temperature covariate or cumulative upwelling at 45^o N. Neither NPI nor PNI were significant in any of the models. The term "significant bivariate model" means that based on the weighted t-test, both coefficients were significantly different from zero.

The four significant models in the bivariate analysis that were examined more closely were 1) summer average temperature - 45^o N June upwelling conditions model, 2) summer average temperature - Northern upwelling extent model, 3) summer average SST - 48^o cumulative upwelling, and 4) Northern upwelling extent - June temperature model. These models were chosen because out of all the significant bivariate models the covariates in these models were not highly correlated (see Table 2). Plots of survival versus the covariates are shown in Figures 17 - 20, using the covariate values from Humptulips Hatchery for the summer average temperature - 45^o N June upwelling model, and covariate values from Bingham Creek (Simpson) Hatchery for the summer average temperature

TABLE 5. A table showing the summary of the bivariate model average regression coefficients, by region and the average across all hatcheries. Shaded regions indicate significant averages at the $\alpha = 0.10$ level.

	SUMMER TEMPERATURE - $\hat{\hat{\beta}}_1$							
	June temperature - $\hat{\hat{\beta}}_2$		NPI - $\hat{\hat{\beta}}_2$		PNI - $\hat{\hat{\beta}}_2$		45 N June upwell. - $\hat{\hat{\beta}}_2$	
Region	**Summer Tempt. $\hat{\hat{\beta}}_1$**	**June temp $\hat{\hat{\beta}}_2$**	**Summer Temp. - $\hat{\hat{\beta}}_1$**	**NPI - $\hat{\hat{\beta}}_2$**	**Summer Temp. - $\hat{\hat{\beta}}_1$**	**PNI - $\hat{\hat{\beta}}_2$**	**Summer Temp. - $\hat{\hat{\beta}}_1$**	**45 N June - $\hat{\hat{\beta}}_2$**
Strait of Juan de Fuca								
Coefficient estimate	-0.00419	-0.05117	-0.06348	0.04548	0.01698	-0.10066	0.02438	0.00007
p - value	0.694	0.029	0.894	0.100	0.932	0.005	0.0957	0.965
Coastal Hatcheries								
Coefficient estimate	-0.11698	0.01052	-0.12512	-0.00544	-0.12543	0.03244	-0.12708	0.00120
p - value	<0.001	0.010	<0.001	0.001	<0.001	0.251	<0.001	0.004
Lower Columbia								
Coefficient estimate	-0.06534	0.05880	-0.12111	-0.0108	-0.11678	0.02181	-0.08852	0.00127
p - value	0.243	0.053	0.023	0.110	0.017	0.55	0.173	0.011
Overall Average								
Coefficient estimate	-0.0914	0.01058	-0.1196	0.00557	-0.09344	0.00873	-0.11865	0.00014
p - value	0.001	0.060	<0.001	0.505	0.031	0.416	<0.001	0.003

TABLE 5. (continued)

Region	SUMMER TEMPERATURE							
	45 N Summer Upwelling - $\hat{\beta}_2$		48 N June Upwelling - $\hat{\beta}_2$		48 N Summer Upwelling - $\hat{\beta}_2$		Northern Upwelling Extent- $\hat{\beta}_2$	
	Summer Temp. - $\hat{\beta}_1$	**45 N Summer - $\hat{\beta}_2$**	**Summer Temp. - $\hat{\beta}_1$**	**48 N June - $\hat{\beta}_2$**	**Summer Temp. - $\hat{\beta}_1$**	**48 N Summer - $\hat{\beta}_2$**	**Summer Temp. - $\hat{\beta}_1$**	**Northern Extent - $\hat{\beta}_2$**
Strait of Juan de Fuca								
Coefficient estimate	0.02134	0.00511	-0.02552	0.00027	-0.10932	0.0091	0.00685	-0.01551
p - value	0.961	0.084	0.946	0.500	0.809	<0.001	0.987	0.989
Coastal Hatcheries								
Coefficient estimate	-0.1227	-0.000003	-0.12270	0.00214	-0.11735	0.00044	-0.12407	0.04208
p - value	<0.001	0.979	<0.001	0.037	<0.001	0.689	<0.001	0.037
Lower Columbia								
Coefficient estimate	-0.13532	0.00127	-0.11686	0.00127	-0.10754	-0.00314	-0.11671	0.07077
p - value	0.013	0.011	0.006	0.011	<0.001	0.429	0.216	0.035
Overall Average								
Coefficient estimate	-0.11932	0.0001	-0.11331	0.00015	-0.09324	0.00054	-0.07847	0.04334
p - value	<0.001	0.014	<0.001	0.049	0.002	0.567	0.101	0.011

TABLE 5. (continued)

Region	SUMMER TEMPERATURE - $\hat{\hat{\beta}}_1$				NORTHERN UPWELLING EXTENT - $\hat{\hat{\beta}}_1$			
	45 N Cumulative Upwelling - $\hat{\hat{\beta}}_2$		48 N Cumulative Upwelling - $\hat{\hat{\beta}}_2$		June Temperature - $\hat{\hat{\beta}}_2$		NPI - $\hat{\hat{\beta}}_2$	
	Summer Temp. $\hat{\hat{\beta}}_1$	45 N Cumul. Upwelling - $\hat{\hat{\beta}}_2$	Summer Temp. - $\hat{\hat{\beta}}_1$	48 N Cumul. Upwelling - $\hat{\hat{\beta}}_2$	Northern Extent $\hat{\hat{\beta}}_1$	June Temp. - $\hat{\hat{\beta}}_2$	Northern Extent - $\hat{\hat{\beta}}_1$	NPI - $\hat{\hat{\beta}}_2$
Strait of Juan de Fuca								
Coefficient estimate	0.09028	0.00050	0.01274	0.00082	0.02967	-0.02277	-0.03179	0.04943
p - value	0.912	0.773	0.981	0.127	0.830	0.888	0.353	0.058
Coastal Hatcheries								
Coefficient estimate	-0.30920	-0.00072	-0.17620	-0.00085	0.03994	-0.05445	0.05597	-0.0146
p - value	0.198	0.006	0.011	0.0223	0.013	0.001	0.002	0.002
Lower Columbia								
Coefficient estimate	-0.05028	-0.00059	-0.06980	-0.00128	0.12923	0.12882	0.12882	-0.03511
p - value	0.059	0.708	0.141	0.046	0.025	0.083	0.083	0.023
Overall Average								
Coefficient estimate	-0.29487	-0.00051	-0.12004	-0.00080	0.04560	-0.03784	0.05307	-0.00880
p - value	0.082	0.252	0.037	0.064	0.081	0.012	0.175	0.66

TABLE 5. (continued)

Region	NORTHERN UPWELLING EXTENT - $\hat{\hat{\beta}}_1$							
	PNI - $\hat{\hat{\beta}}_2$		45 N June Upwelling - $\hat{\hat{\beta}}_2$		45 N Summer Upwelling - $\hat{\hat{\beta}}_2$		48 N June Upwelling - $\hat{\hat{\beta}}_2$	
	Northern Extent - $\hat{\hat{\beta}}_1$	**PNI - $\hat{\hat{\beta}}_2$**	**Northern Extent - $\hat{\hat{\beta}}_1$**	**45 N June - $\hat{\hat{\beta}}_2$**	**Northern Extent - $\hat{\hat{\beta}}_1$**	**45 N Summer - $\hat{\hat{\beta}}_2$**	**Northern extent - $\hat{\hat{\beta}}_1$**	**48 N Summer - $\hat{\hat{\beta}}_2$**
Strait of Juan de Fuca								
Coefficient estimate	-0.00780	-0.08141	0.03153	-0.00067	0.00330	0.00391	0.02737	-0.00071
p - value	0.969	0.464	0.916	0.847	0.988	0.832	0.909	0.799
Coastal Hatcheries								
Coefficient estimate	0.02062	0.05545	0.01530	0.00150	0.03151	-0.0022	0.01633	0.00166
p - value	0.351	0.416	0.112	0.003	0.06	0.312	0.024	0.127
Lower Columbia								
Coefficient estimate	0.12916	0.07681	0.11903	-0.00116	0.09870	0.00828	0.12561	-0.00224
p - value	0.261	0.347	0.032	0.602	0.602	0.940	0.224	0.572
Overall Average								
Coefficient estimate	0.03165	0.04185	0.04336	0.00022	0.03545	0.00129	0.03917	0.00020
p - value	0.407	0.416	0.144	0.796	0.321	0.412	0.244	0.848

TABLE 5. (continued)

	NORTHERN UPWELLING EXTENT - $\hat{\hat{\beta}}_1$					
	48 N Summer Upwelling - $\hat{\hat{\beta}}_2$		45 N Cumulative Upwelling - $\hat{\hat{\beta}}_2$		48 N Cumulative Upwelling - $\hat{\hat{\beta}}_2$	
Region	**Northern Extent -** $\hat{\hat{\beta}}_1$	**48 N Summer -** $\hat{\hat{\beta}}_2$	**Northern Extent -** $\hat{\hat{\beta}}_1$	**45 N Cumul. Upwelling -** $\hat{\hat{\beta}}_2$	**Northern Extent -** $\hat{\hat{\beta}}_1$	**48 N Cumul. Upwelling -** $\hat{\hat{\beta}}_2$
Strait of Juan de Fuca						
Coefficient estimate	0.02577	0.00494	0.00910	0.00020	-0.00793	0.00037
p - value	0.818	0.231	0.956	0.253	0.905	0.142
Coastal Hatcheries						
Coefficient estimate	0.04081	-0.00020	0.04946	-0.0043	0.04647	-0.00104
p - value	0.028	0.963	<0.001	0.004	0.032	0.427
Lower Columbia						
Coefficient estimate	0.09686	-0.00342	0.13427	-0.00131	0.11492	-0.00184
p - value	0.077	0.868	0.131	0.348	0.28	0.230
;Overall average						
Coefficient estimate	0.05292	-0.00027	0.06905	-0.00060	0.06367	-0.00094
p - value	0.017	0.949	0.059	0.095	0.104	0.190

- Northern upwelling extent model, and the Northern upwelling extent - June temperature model. These hatcheries were selected for illustration because the covariate values in the models are close to the overall averages, and would thus represent the behavior of the bivariate models for coefficient values of the overall average. Values of the regression coefficients for all hatcheries, and the form for each bivariate proportional hazards model are given in Appendix E.

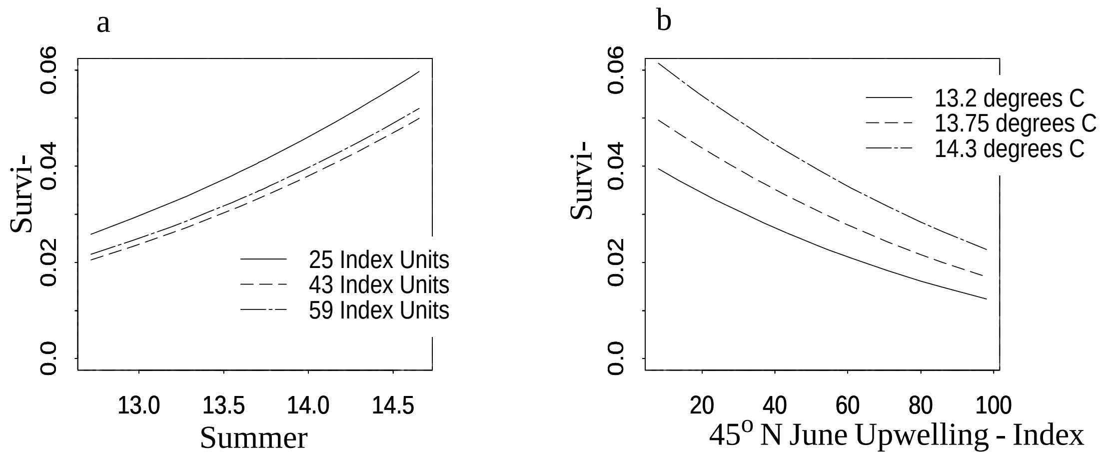

FIGURE 17. Plots showing the relationship between survival and the covariates in of summer temperature and 45^{o} June upwelling strength. The lines in the first plot (a) show the effect of temperature on survival for different June upwelling strengths. The lines in the second plot show the relationship of survival and upwelling for different temperatures. Both plots exhibit increasing survival with increasing temperature and decreasing upwelling strength.

Determination of model fit for the bivariate models was difficult because of the multivariate nature of the data. Therefore, to assess how well the models fit the data, plots were made of the total number of observed adults returns (all age classes) versus the total number of expected adult returns (from all age classes) as predicted by the model. The Bingham Creek (Simpson) Hatchery was chosen to illustrate the plots as the returns from this hatchery seemed to modeled the best out of all the hatcheries, and it had among the greatest number of years of data of any hatchery. The plots in Figure 21 show observed versus expected numbers of adult returns for the four significant models. For well fitted

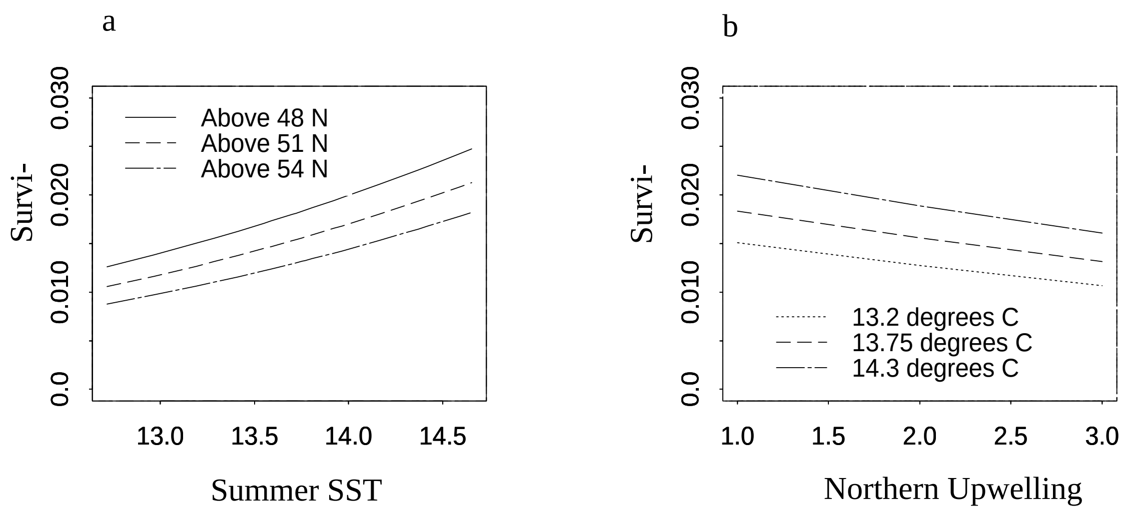

FIGURE 18. Plots exhibiting the relationship between survival and the bivariate model of summer seas surface temperature (SST) and northern extent. The lines in the first plot (a) show the effect of temperature on survival of coho to two years old as June upwelling conditions move further north. The lines in second plot (b) show the effect of the northern limit of upwelling for different summer SST values.

models, the points in the graphs should fall along the 45^{o} line, represented by the dashed line, and the difference between the observed and expected values (residual deviance) would be close to zero.

Tables 6 - 9 give the sums of residual deviancies, and sums of squared residual deviance for the bivariate models, and the associated univariate models in order to compare how well the models fit the data. The sum of the residual deviance is a rough indication if the model is over or under estimating the return number. The sum of the squared deviance is an indication of how widely the estimates vary from the observed values; the higher the squared deviance, the further away the model is estimating return number. Lower sums of squared deviance or absolute sums of residual deviancies are preferable over higher sums of squared deviancies or absolute sums residual deviancies for a fitted model. More importantly, a lower sums of squared residual deviance indicates that the

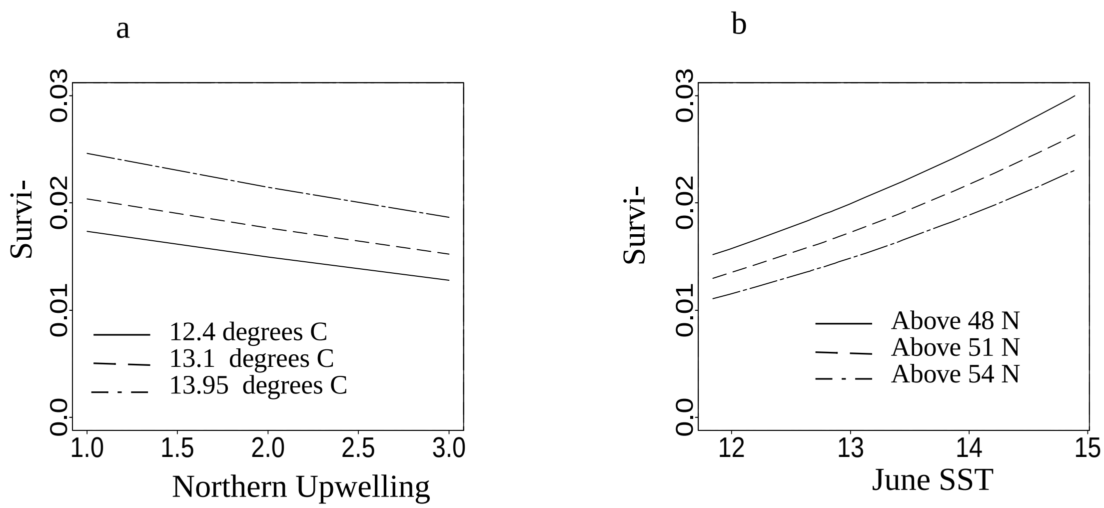

FIGURE 19. Plots showing the relationship between survival and the covariates in the bivariate model with northern upwelling extent and June sea sruface temperature (SST). The lines in first plot (a) show for different June temperature values, the effect on survival as upwelling conditions occur further north in June. The lines in the second plot (b) shows the effect of June temperature for the different locations of June upwelling. Both plots show a decrease in survival with increasing northward occurrences of June upwelling and an increase in survival with increasing June SST.

addition of the second covariate accounted for more of the variability in adult returns than single covariate in the univariate model.

Residual plots for the Summer temperature - 45^{o} N June upwelling model are shown in Figure 22. Both univariate and bivariate model residual plots are given to compare model fit for the two covariates. In the bivariate case, the points seem more evenly scattered about the x-axis (dotted line). The points also seem closer to the x-axis in the bivariate case meaning that more of the data variability is explained by the addition of the second covariate. The squared residual deviancies for the Summer temperature - 45^{o} N June upwelling model appear in Table 6 along with the deviancies for each of the associated univariate models. There were only four hatcheries with a lower residual deviance for the bivariate model than for the univariate models. Eight of the hatcheries had a lower

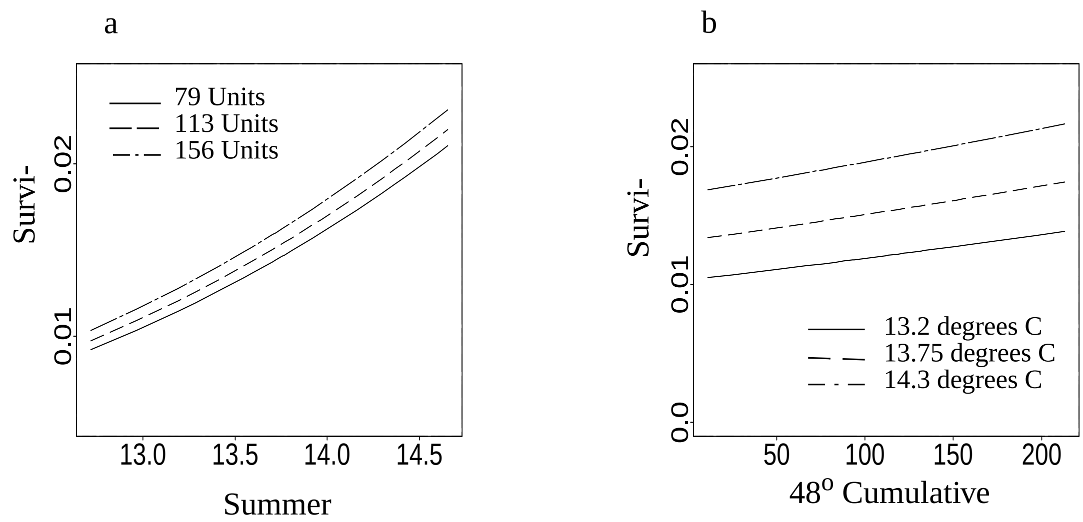

FIGURE 20. Plots showing the relationship between survival and the covariates in the bivariate model with summer sea surface temperature (SST) and 48º cumulative upwelling. The lines in the first plot (a) show the effect of summer SST on coho survival at three different level of cumulative upwelling. The lines in the second plot (b) show the effect of increases in cumulative upwelling for three different values of summer SST. Both plots show an increase in survival with increasing summer SST and increasing cumulative upwelling values.

squared deviance than the univariate models, but only four hatcheries showed a reduction in both measures of residual deviance from the associated univariate models. Only eight out of thirteen hacheries showed a reduction in at least one of the residual deviance measures, which was not enough hatcheries to consider this model further.

Figure 23 shows the residual plots for the Summer SST-Northern Extent bivariate model. The points in the bivariate plots seem more centered around the x-axis (dotted line) than in univariate models, indicating a decrease in bias. Diagnostic residual plots for the Northern upwelling extent - June temperature model appear in Figure 24. Again, the points are more evenly scattered about 0 in the bivariate case than in the univariate plots. However, there appears to be a curvilinear trend in the plots of June temperature versus the residuals, indicating that the relationship between survival and June SST is non-linear,

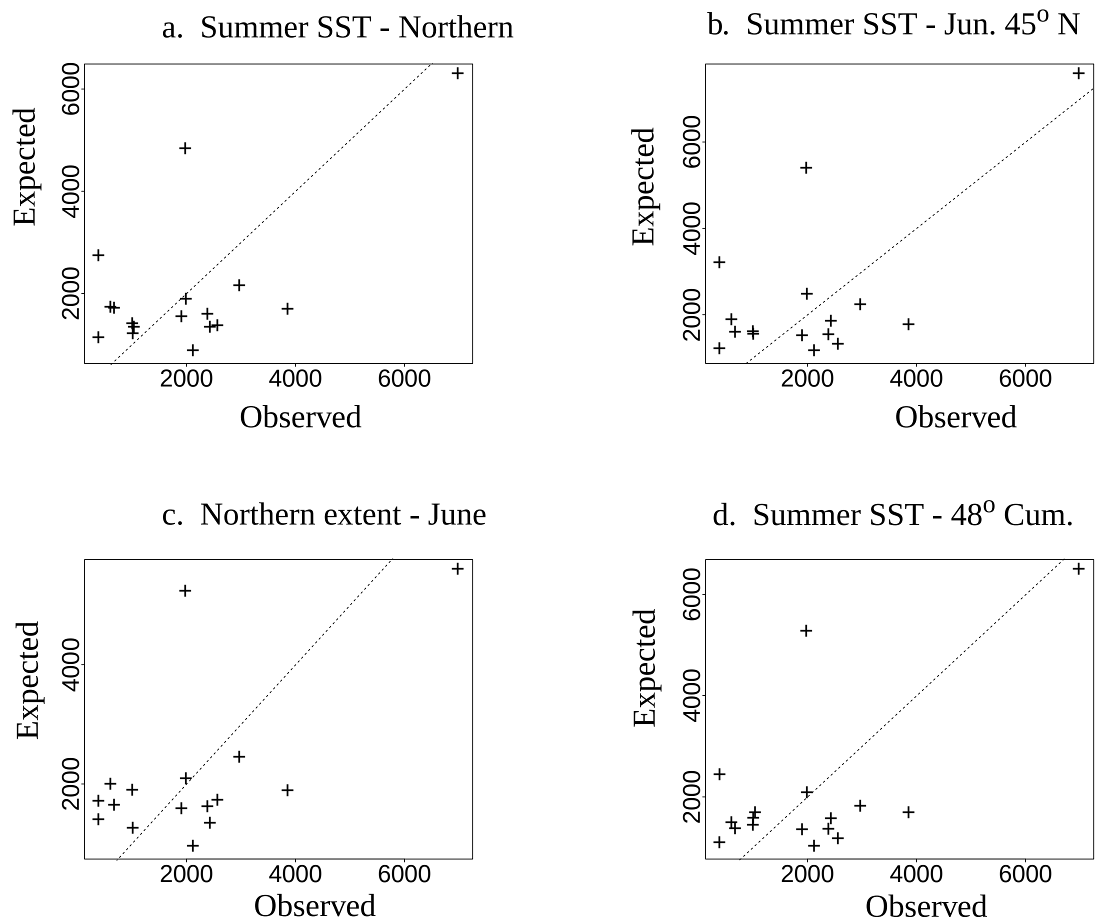

FIGURE 21. Plot of observed versus expected total adult returns for the Bingham Creek Hatchery for the models summer temperature and Northern extent (a), summer SST and 45° N June upwelling (b), Northern extent and June temperature (c) and summer SST and 48° N cumulative upwelling. The dotted line represents the 45° line. If the model fits the data well, one would expect the points to fall closely along this line.

which was confirmed by the significance of the June SST quadratic model. The residual deviance for the Summer SST-Northern extent model appear in Table 7, and for the Northern Extent-June SST model in Table 8. Although Table 7 shows seven hatcheries as having a reduction in the sum of squared deviance for the Summer SST-Northern extent model over the univariate models, only two hatcheries show a reduction in the sum of residual

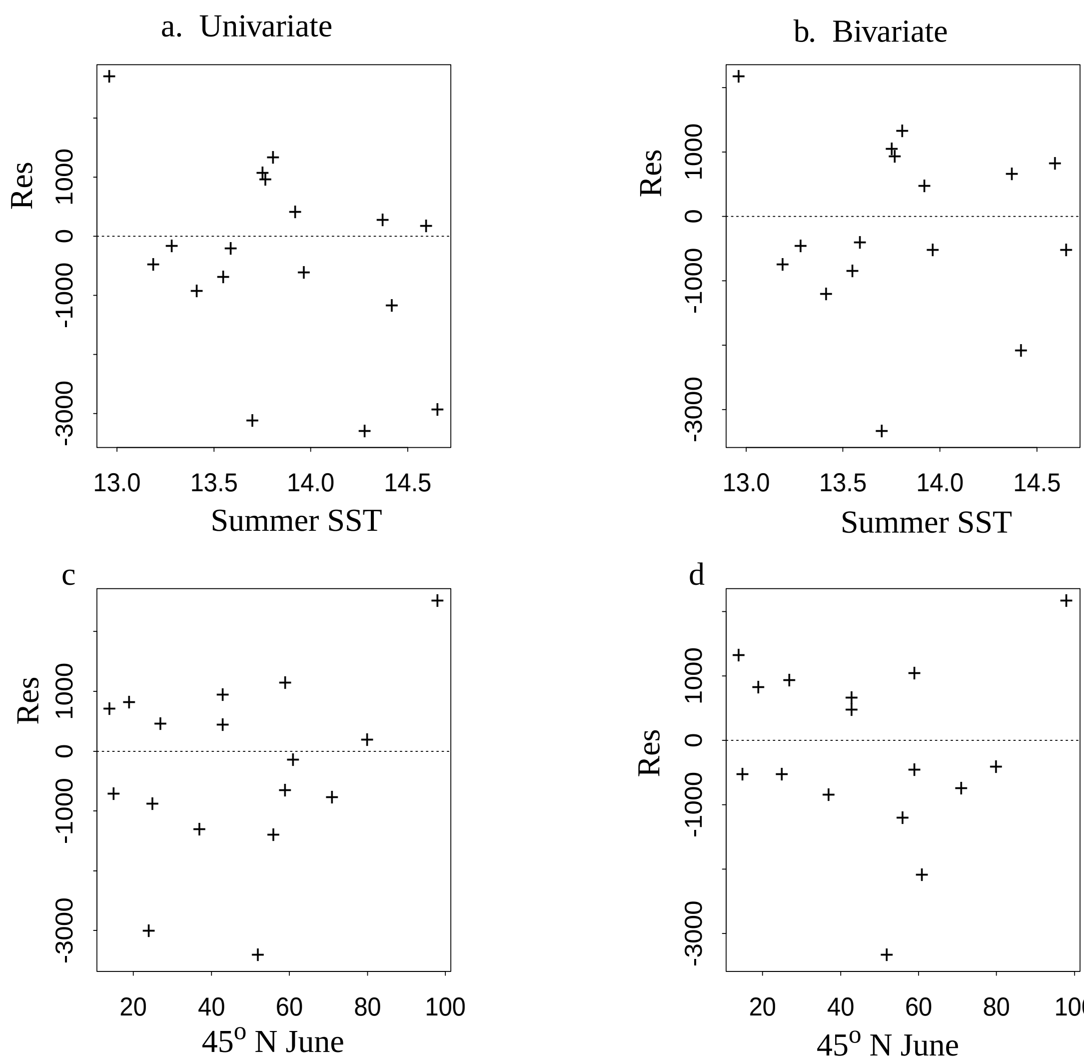

FIGURE 22. Diagnostic residual plots for the Summer sea surface temperature (SST)- 45^{o} N June upwelling model for the Simpson (Bingham Creek) Hatchery. The plots show the covariate values versus the residual values (observed values minus expected values) for both the univariate (a and c) and bivariate models (b and d). In both cases, the bivariate models exhibit less bias (points are more evenly distributed above and below the 0 line), and are closer to the line representing residual values equal to zero. The sum of the residual deviance was reduced from -7389.9 and -5697.5 in the univariate models to only 6.23 in the bivariate model, reflecting the change seen in the plots.

TABLE 6. Table showing the sums of the residual deviance and squared deviance values for the univariate models of summer sea surface temperature (SST) and 45^o N June upwelling, and the summer (SST)/45^o N June upwelling, bivariate model. Associated residual plots are shown in Figure 22. Shaded areas indicate a bivariate model with values closer to zero (lower absolute value) than either univariate model.

Hatchery	Summer SST		45^o North Upwelling		Bivariate Model -	
	Deviance	Squared Deviance	Deviance	Squared Deviance	Deviance	Squared Deviance
Strait of Juan de Fuca Region						
Dungeness	1.01	6.53e+07	0.81	6.17e+07	-3.33	6.49e+07*
Lower Elwha	3.25	2.71e+06	0.15	3.88e+06	2.43*	2.80e+06*
Coastal Region						
Soleduc	23.03	7.72e+07	17.51	7.92e+07	-0.26	8.05e+07
Quinault Lake	11.68	1.39e+07	50.25	1.53e+07	5.87	1.00e+07
Quinault NFH	3.03	1.25e+07	2.36	1.86e+07	24116	5.00e+07
Humptulips	0.74	3.37e+07	1.47	3.96e+07	28080	1.24e+08
Simpson	-7389.9	4.46e+07	-5697.5	3.72e+07	6.23	2.33e+07
Willapa	-17.66	3.59e+07	0.78	3.92e+07	-60.98	3.29e+07
Lower Columbia Region						
Grays River	0.47	1.97e+07	-0.56	2.09e+07	-18409	5.18e+07
Elochomin	1005.16	9.06e+06	2.05	6.75e+06	-5.82*	5.80e+06
Cowlitz	-2.02	9.25e+07	3.15	9.00e+07	-0.50	9.00e+07
Toutle River	267.12	4.20e+07	8.18	2.78e+07	2952.28	1.05e+07
Washougal	-4.74	3.28e+08	-2.86	3.41e+08	3.41*	3.09e+08

* Indicates a bivariate model with lower values than only one of the univariate models.

deviance values. Alternately, the Northern Extent-June SST model bivariate model reduced the sum of squared residual deviances at ten of the hatcheries, and the sum residual deviances at four of the hatcheries. Of the two models with northern upwelling extent, the model with June SST explains more of the variability, across more hatcheries than the bivariate model with Summer SST.

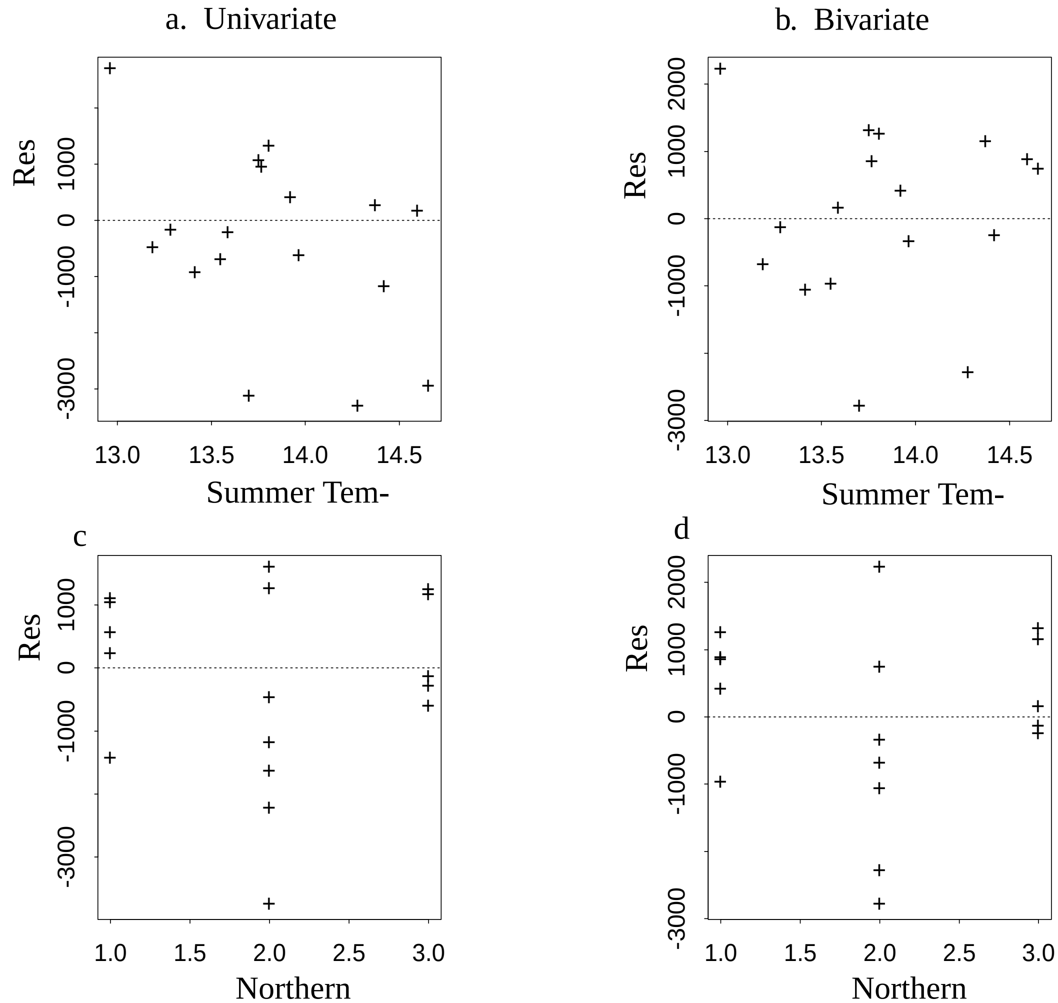

FIGURE 23. Diagnostic residual plots for the Summer temperature - northern extent model for the Simpson (Bingham Creek) Hatchery. The plots show the covariate values versus the residual values (observed values minus expected values) for both the univariate (a and c) and bivariate models (b and d). The residual values are more evenly scattered about the x-axis in the bivariate plots (b and d) than in the univariate plots (a and c), with a change the sum of residual deviance from -7389.9 and -4008 in the univariate models to 6.83 in the bivariate model (Table 7).

TABLE 7. Table showing the sums of the residual deviance and squared deviance values for the univariate models of summer sea surface temperature (SST) and Northern upwelling extent, and the summer SST/Northern upwelling extent, bivariate model. Associated residual plots are shown in Figure 23. Shaded areas indicate a bivariate model with values closer to zero (lower absolute value) than either univariate model.

Hatchery	Summer SST		Northern Upwelling Extent		Bivariate Model	
	Deviance	Squared Deviance	Deviance	Squared Deviance	Deviance	Squared Deviance
Strait of Juan de Fuca Region						
Dungeness	1.01	6.53e+07	-8.95	5.21e+07	-73.77	5.24e+07
Lower Elwha	3.25	2.71e+06	2.33	3.42e+06	3.06*	2.73e+06*
Coastal Region						
Soleduc	23.03	7.72e+07	20.47	8.70e+07	3546	7.91e+07*
Quinault Lake	11.68	1.39e+07	51.90	1.47e+07	165.77	1.22e+07
Quinault NFH	3.03	1.25e+07	-2.56	2.05e+07	4.71	1.25e+07
Humptulips	0.74	3.37e+07	0.95	4.30e+07	32.10	3.31e+07
Simpson	-7389.9	4.46e+07	-4008	3.58e+07	6.83	2.76e+07
Willapa	-17.66	3.59e+07	-0.47	3.91e+07	25.76	3.18e+08
Lower Columbia Region						
Grays River	0.47	1.97e+07	6.18	1.33e+07	7.37	1.34e+07*
Elochomin	1005.2	9.06e+06	-9.47	6.12e+06	112.12*	4.32e+05
Cowlitz	-2.02	9.25e+07	-3.62	9.28e+07	-4.26	9.46e+07
Toutle River	267.1	4.20e+07	0.63	4.27e+07	0.34	4.31e+07
Washougal	-4.74	3.28e+08	-1.67	3.49e+08	-4.75	3.18e+08

* Indicates a bivariate model with lower values than only one of the univariate models.

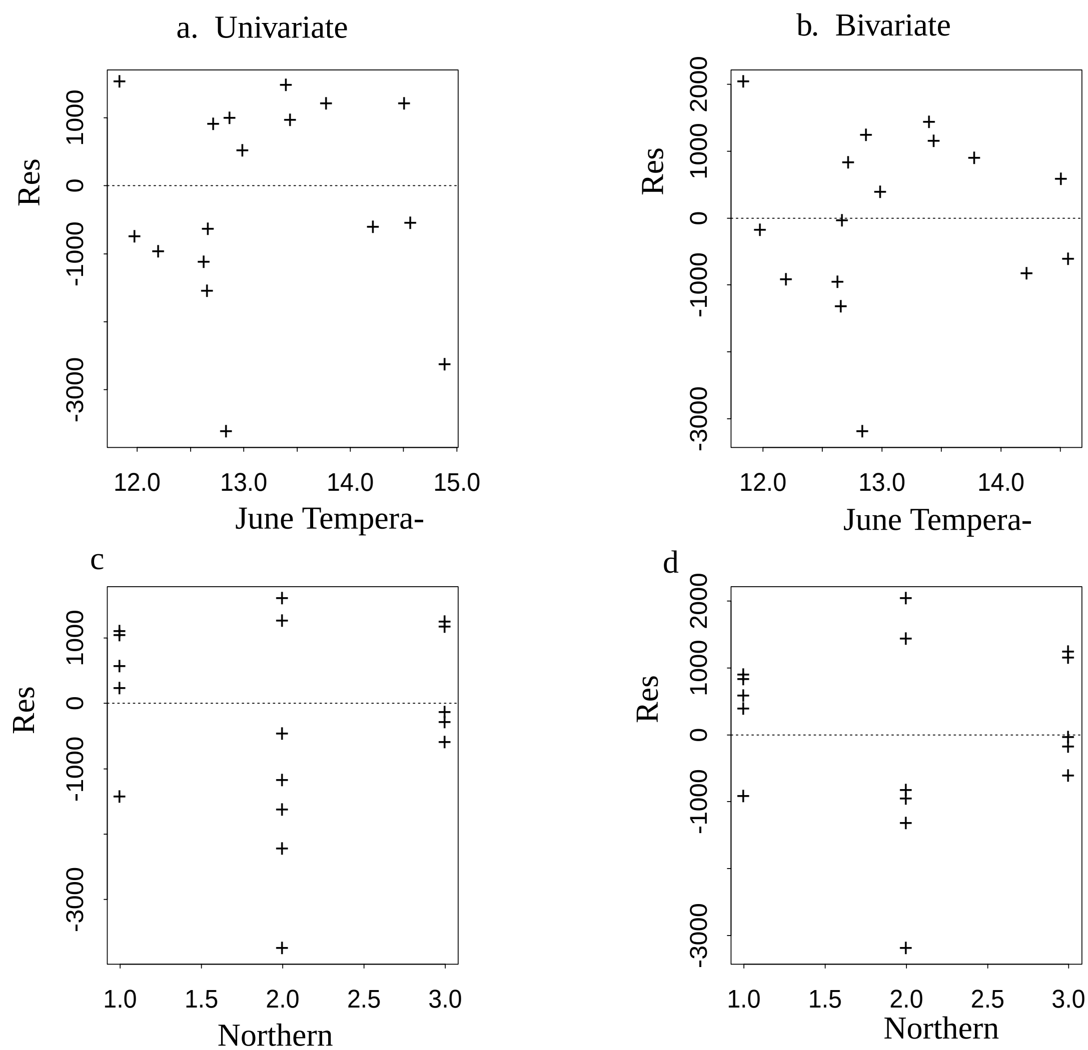

FIGURE 24. Diagnostic residual plots for the univariate and bivariate models of June sea surface temperature (SST) and northern upwelling extent for the Simpson (Bingham Creek) Hatchery. The plots of the first column (a and c) show the residuals of the univariate model versus each of the covariates. The plots in the second column (b and d) show the residuals from the bivariate model plotted against the covariate values. The residuals for the bivariate model were more centered about zero, reflected in a sum of the residual deviance of 19.58, versus -4008.41 and -4100.75 for the June SST and northern extent univariate models (Table 8). The sum of the squared deviance was also reduced in the bivariate model to 2.58×10^{-7}.

TABLE 8. Table showing the sums of the residual deviance and squared deviance values for the univariate models of Northern upwelling extent and June sea surface temperature (SST), and the Northern upwelling extent/ June (SST), bivariate model. Associated residual plots are shown in Figure 22. Shaded areas indicate a bivariate model with values closer to zero (lower absolute value) than either univariate model.

Hatchery	Northern Upwell Extent		June SST		Bivariate Model	
	Deviance	Squared Deviance	Deviance	Squared Deviance	Deviance	Squared Deviance
Strait of Juan de Fuca Region						
Dungeness	-8.95	5.21e+07	1.17	5.05e+07	1.60*	4.41e+07
Lower Elwha	2.33	3.42e+06	121.41	3.49e+06	4.12*	2.69e+06
Coastal Region						
Soleduc	20.47	8.70e+07	19.43	7.59e+07	-15.38	8.83e+07
Quinault Lake	51.90	1.47e+07	50.27	1.55e+07	-0.57	1.12e+07
Quinault NFH	-2.56	2.05e+07	-3.65	1.96e+07	24.72	1.67e+07
Humptulips	0.95	4.30e+07	-0.18	3.96e+07	29.16	3.53e+07
Simpson	-4008.4	3.58e+07	-4100.7	3.69e+07	19.58	2.58e+07
Willapa	-0.47	3.91e+07	2293.50	3.89e+07	-958.9*	3.77e+07
Lower Columbia Region						
Grays River	6.18	1.33e+07	0.95	2.08e+07	2.45*	1.34e+07
Elochomin	-9.47	6.12e+06	-1.21	9.00e+06	-11.08	6.23e+06*
Cowlitz	-3.62	9.28e+07	-2.19	9.53e+07	63849	4.24e+08
Toutle River	0.63	4.27e+07	-24.58	2.58e+07	-0.38	6.22e+06
Washougal	-1.67	3.49e+08	-1709.1	3.21e+08	-11716	2.87e+08

* Indicates a bivariate model with lower values than only one of the univariate models.

Diagnostic residual plots for the summer SST - 48^{o} N cumulative upwelling model are shown in Figure 25. The plots show a large reduction in bias from the univariate cumulative upwelling model to the bivariate model (Figure 25c and 25d), and a slight reduction in bias from the summer SST model. The sums of the residual deviances and sums of squared residual deviances for the bivariate model and associated univariate models are shown in Table 9. Seven of the thirteen hatcheries had a reduction in the sum of residual deviance over both to the univariate models, while ten hatcheries had a reduction in the sum of squared residual deviances. Of all the bivariate models, the Summer SST-48^{o} N cumulative upwelling model had a reduction of deviance in the greatest number of hatcheries.

Discussion

Model and methods

The data analysis presented here represents a way to model first year ocean survival and investigate survival relationships. All model parameters were estimated from the coded wire tag data alone. Estimates of fishing effort and tag recovery effort were not required, which was one advantage of the model, and prior assumptions or estimates of model parameters from auxiliary data were unnecessary, a second advantage of the model. A disadvantage of the model was the limited number of regression parameters that could be estimated in a model. The overall behavior of the model, the advantages and disadvantages of the method and the results of the data analysis will be discussed in the following section.

There were several major points coming out of the analysis of CWT data using the multinomial model. The first was the need to look at more than one hatchery, or even more than one region to ascertain the effect of a covariate on ocean survival, as was proven by the data analysis and shown clearly in the results section. A second point was the degree of variability and quality of the CWT data. A third issue was the lack of sufficient numbers of brood years marked with CWTs at an adequate number of hatcheries to estimate the parameters of a models with more than two covariates. The above three issues combined to restrict the number of covariates in a model.

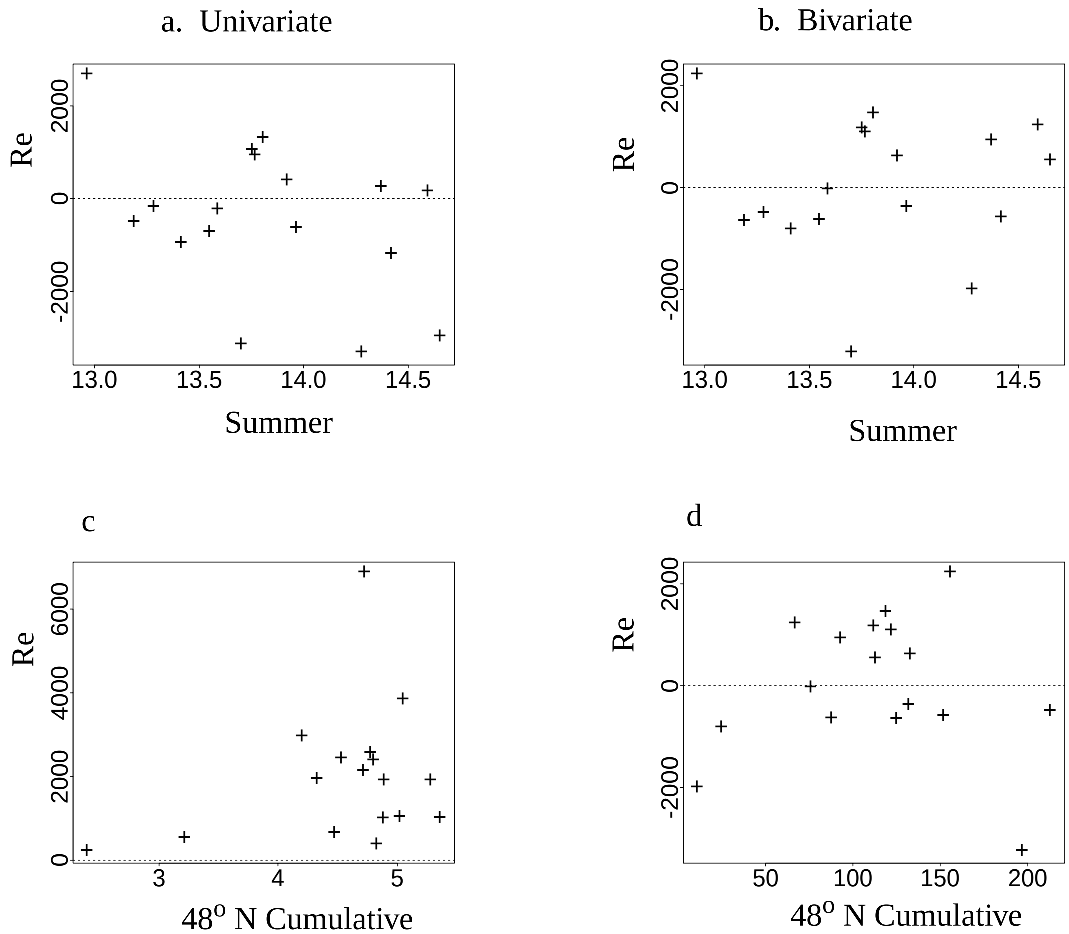

FIGURE 25. Diagnostic residual plots for the summer sea surface temperature (SST) - 48^{o} N cumulative upwelling model. The first column of plots (a and c) show the univariate model residuals versus each of the covariates. The plots in the right column (b and d) show the residuals from the bivariate model plotted against the covariates. The residual values are more evenly scattered about the y-axis (dotted line) in the bivariate model than in either of the univariate models. The change is reflected in the sum of residual deviances, with a value of -2.66 for the bivariate model and values of -7389.8 and 33349 for the univariate models of Summer SST and 48^{o} N cumulative upwelling, respectively (Table 9).

TABLE 9. Table showing the sums of the residual deviance and squared residual deviance values for the univariate models of Summer sea surface temperature (SST) and 48^{o} N cumulative upwelling, and the Summer temperture/48^{o} N cumulative upwelling, bivariate model. Associated residual plots are shown in Figure 25. Shaded areas indicate a bivariate model with values closer to zero (lower absolute value) than either univariate model.

Hatchery	Summer SST		48^{o} N Cumulative Upwelling		Bivariate Model	
	Deviance	Squared Deviance	Deviance	Squared Deviance	Deviance	Squared Deviance
Strait of Juan de Fuca Region						
Dungeness	1.01	6.53e+07	0.64	6.33e+07	-0.20	5.24e+07
Lower Elwha	3.25	2.71e+06	-0.72	3.75e+06	6.03	2.31e+06
Coastal Region						
Soleduc	23.03	7.72e+07	-27.61	7.71e+07	7.89	7.59e+07
Quinault Lake	11.68	1.39e+07	-5.44	1.51e+07	12.28	1.39e+07
Quinault NFH	3.03	1.25e+07	-22.28	1.76e+07	0.43	1.11e+07
Humptulips	0.74	3.37e+07	-5.93	3.95e+07	-22.93	2.79e+07
Simpson	-7389.8	4.46e+07	33349	3.61e+07	-2.66	2.94e+07
Willapa	-17.66	3.59e+07	-0.69	2.42e+07	-0.19	2.43e+07
Lower Columbia Region						
Grays River	0.47	1.97e+07	-6.33	2.21e+07	4.67*	2.02e+07*
Elochomin	1005.16	9.06e+06	2.13	7.13e+06	7.08*	5.85e+06
Cowlitz	-2.02	9.25e+07	-14.25	9.09e+07	1.85	8.78e+07
Toutle River	267.12	4.20e+07	-39.07	1.14e+07	-31.28	1.99e+07*
Washougal	-4.74	3.28e+08	-9.87	1.93e+08	403.65	1.93e+08

* Indicates a bivariate model with lower values than only one of the univariate models.

Each model had a minimum of five parameters to estimate, requiring at least six degrees of freedom, or six years of data. The optimization program converged more readily with more years of data, and would yield estimates over a wider range of covariates. Therefore, seven years of data was used as the minimum number of years of data required from any one hatchery. Only fifteen different hatcheries, out of a possible 24 from the Strait of Juan de Fuca, Coastal and Lower Columbia River regions, had seven or more years of data (Table 1), and thus could be used in the univariate analysis. Only thirteen hatcheries were used in the bivariate analysis, which has six estimable parameters, requiring at least eight years of data. With highly variable data, precise paratmeter estimates require numerous years of data. The lack of hatcheries with adequate data restricted the number of parameters that could be estimated in a model, thus restricting the number of covariates in the model. This is the reason why interactions between parameters were not investigated.

The need to look at and interpret the results from more than one hatchery was apparent from the results. Individual hatchery results for both the univariate, quadratic, and bivariate models are presented in Appendices C, D and E. Figures 9 - 14 show the fitted regression lines for coastal and lower Columbia River hatcheries. The plots of the fitted lines best exemplify the variability in results within regions and between regions. The weighted t-test seems to have been an adequate way to resolve conflicting model results. Regression coefficients that were estimated with more precision were given more weight when calculating the weighted mean and the standard error of the mean regression coefficient, $\hat{\bar{\beta}}$. Covariates displaying a consistent effect across all hatcheries were found to be significant in the weighted t-test analysis. The results of the t-test were also confirmed by the plots of the raw data, giving further support of this method.

Like all regression models, variability in results is directly related to variability in the data. CWT data is collected in the fishery, at the hatchery and by voluntary tag returns in the recreational fishery. Release numbers are probably more accurately known than return numbers, because the fish are generally tagged and released at the hatchery under controlled conditions. However, observed CWT returns come from several different areas and from several different agencies, so the probability of reporting errors are likely. In addition, only a fraction of the catch is sampled and examined for tags, and so there is added error from the sampling fraction. Therefore, sources of variability would more likely be due to errors in return numbers than errors in release numbers. Errors in release or return counts would bias the survival estimates. An underestimate of return numbers would lead to an underestimation of survival, while an overestimation of return numbers would artificially inflate survival estimates. Additionally, tag loss numbers are not reported because they are not well estimated (WA State Progress Report, 1984 - 1992). It is highly likely that more tagged fish are recovered than recorded, leading to an underestimation of survival.

The three nuisance parameters in the model, M_2, θ_1, and θ_2 will not be discussed at length. The values for the parameters are given in Appendix E, by hatchery. The parameters were held constant across all brood years for each hatchery. However in looking at the CWT data (Appendix A), there seems to be much variability in the number of two and four year old returns between brood years. This may account for the large residual deviance in the models, even though the survival curves seemed to fit the data.

A limitation of the model is the inability to perform an Analysis of Deviance, which involves checking the regression model against either a grand mean model or a fully specified model. The full model is one in which the two-year old survival parameter is estimated for each brood year, and would be given by,

$$L(\underset{\sim}{S_2}, M_2, \theta_1, \theta_2 | R_i, t_{i2}, t_{i3}, t_{i4}) = \prod_{i=1}^{n} (S_{i2}, M_2, \theta_1, \theta_2 | R_i, t_{i2}, t_{i3}, t_{i4}) \,, \quad \text{(EQ 19)}$$

where i is a brood year. Age two survival is modelled as varying year to year in the full model. A grand mean model would be one in which two-year old survival is estimated as being constant across all brood years, and is given by,

$$L(S_2, M_2, \theta_1, \theta_2 | R_i, t_{i2}, t_{i3}, t_{i4}) = \prod_{i=1}^{n} (S_2, M_2, \theta_1, \theta_2 | R_i, t_{i2}, t_{i3}, t_{i4}) \,, \quad \text{(EQ 20)}$$

and age two survival does not vary from year to year, but is estimated as constant across all brood years. The regression model falls between the two models, and allows the variability in age two survival to be a function of environmental conditions. The analysis of deviance examines where the regression model lies in relation to the full and grand mean models. If the value of the log-likelihood from the regression model is closer to log-likelihood value of the full model than it is to the grand mean model, then at least one regression parameter is significantly different from zero, and the regression model is significant. If the log-likelihood values of the grand mean and regression models are close, then the regression coefficients are not significantly different from zero, and the grand mean model best describes the data. How close the values between the log-likelihoods must be in order to reject a null hypothesis of H_o: $\beta_i = 0$ versus H_a: $\beta_i \neq 0$, for all *i*, is a function of the significance level α and the number of parameters in the model. The significance of the regression model is based on an asymptotic F-test (Smith, 1991).

Between year variability can be accounted for in the ANODEV (Smith, 1991). Without a covariate, the multinomial model has only three minimally sufficient statistics, for each brood year. The full model has four parameters for each brood year while grand mean models has only four parameters across all brood years. Therefore, estimating the parameters in the full and grand mean models is not possible, leaving only the parameters of the regression models as estimable. This is the reason why ANODEV could not be used with the coho survival analysis.

Implications of regression results

Four of the eleven covariates had a significant linear relationship with survival, Summer average sea surface temperature (SST), 45^o N June upwelling strength, northern upwelling extent, and 48^o N cumulative upwelling. Three of the covariates, June SST, 45^o N June upwelling strength, and 48^o N cumulative upwelling had a significant quadratic (non-linear) relationship with survival. Of these quadratic relationships, only two are of interest because of the similarities in response among many of the hatcheries. Some of the bivariate models were also significant. Model results, and the implication to ocean survival of coho salmon are discussed in this section.

The significant positive correltaion between age two survival and 48^{o} N cumulative upwelling agree with most of the studies conducted on Oregon coho salmon. Several studies found a positive relationship between cumulative upwelling during the spring and summer in the year of outmigration and coho marine survival (Gunsolus, 1978; Scarnecchia, 1981; Nickelson and Lichatowich, 1984; Mattews, 1984; Nickelson, 1986). A positive association between growth rates of salmon and cumulative upwelling was observed in two studies, one for Oregon coho (Fisher and Pearcy, 1988) and one for coho off the coast of Vancouver Island (Holtby et. al., 1990). However, all of the relationships were assumed stricly linear. The agreement between the results using the multinomial model and the results of previous studies indicates the effectiveness of the model in assess ocean condition and smolt survival relationships.

The most interesting results were found in the analysis of the non-linear relationship between the covariates and survival as represented by the quadratic model. The two covariates of interest are June SST and 48^{o} N cumulative upwelling. Although the overall average of the quadratic term for June SST was non-significant, when the two Strait of Juan de Fuca hatcheries were removed (considering Coastal and Lower Columbia hatcheries only), the mean regression coefficient for the quadratic term became significant ($p = 0.085$). Additionally, the similarity of the survivorship curves both within the regions and between the two regions could not be ignored (Figure 13). The quadratic relationship of survival with 48^{o} N cumulative upwelling was also significant ($p = 0.051$, mean quadratic coefficient). Again there was similarity of the survivorship curves within the Coastal and Lower Columbia hatcheries as shown in Figure 14.

The most striking feature of the June SST quadratic curves (Figure 13) is the alignment of the maxima amount the hatcheries both within and between regions. The maxima of the quadratic PH model for each hatchery are given in Table 10, and were calculated using Eq 18. The maxima occur between 13.07 ^{o}C and 13.71 ^{o}C with a mean of 13.45 ^{o}C and a coefficient of variation of 65%. The coefficients, chi-square value and p-values are given in Table 10, and the standard errors are given in Appendix D. All but two the hatcheries, the Soleduc and Simpson (Bingham Creek) hatcheries, had significant quadratic models at the $\alpha = 0.10$ level.

TABLE 10. A table showing a summary of results for the June sea surface temperature (SST) quadratic model. The summary includes the regression coefficients, the location of the maximum estimated survival as a function of temperature, the chi-square statistic for the model and the p-value for the model for all hatcheries in the Coastal and Lower Columbia River regions.

Hatchery	**Linear Term - $\hat{\beta}_1$**	**Quadratic Term - $\hat{\beta}_2$**	**Maxima**	**Model χ^2 value**	**p-value**
Coastal region:					
Soleduc	-0.014101	0.014969	13.68	0.1241	0.940
Quinault Lake	-0.050436	0.082015	13.54	6.1376	0.046
Quinault NFH	-0.071734	0.071797	13.71	9.5970	0.008
Humptulips	-0.059735	0.150492	13.44	18.027	<0.001
Simpson	-0.016887	0.034113	13.48	2.1698	0.338
Willapa	-0.128679	0.187913	13.57	11.535	0.003
Lower Columbia River region:					
Grays River	-0.058272	0.099341	13.52	7.0779	0.029
Elochomin	-0.284107	0.663607	13.07	43.329	0
Cowlitz	0.003800	0.117797	13.25	49.927	0
Toutle River	-0.083449	0.236840	13.42	30.335	0
Washougal	0.046526	0.230626	13.17	102.44	0

The quadratic relationship between survival and 48^{o} N cumulative upwelling showed less consistency among the hatcheries than June SST, although the coastal region showed the most consistency (Figure 14). A summary of the results for both regions are given in Table 11, including the chi-square and p-values, regression coefficients, and maxima for each hatchery. The maxima for the coastal hatcheries with similar survivorship curves (Table 14) are between 56.33 and 105.36 upwelling units, with an average value of 82.19 upwelling units. The three hatcheries showing agreement in the Lower Columbia region were between 28.51 and 166.18 (mean of 111.40) upwelling units, and showed more variability than the coastal hatcheries. Only five out of eleven of the hatcheries had significant quadratic models at the $\alpha = 0.10$ level, although the mean of the quadratic term across all hatcheries was significant.

TABLE 11. A table showing a summary of the results for the quadratic model with 48^o N cumulative upwelling as the covariate. The summary includes the regression coefficients, the location the location of the maximum estimated survival as a function of cumulative upwelling, the chi-square statistic for the model and the p-value for the model for all hatcheries in the Coastal and Lower Columbia River regions.

Hatchery	**Linear Term - $\hat{\beta}_1$**	**Quadratic Term - $\hat{\beta}_2$**	**Maxima**	**Model χ^2 value**	**p-value**
Coastal Region:					
Soleduc	-1.763185	0.503549	56.33	1.9845	0.371
Quinault Lake	-1.936352	0.514513	76.16	9.0350	0.011
Quinault NFH	-3.934106	0.980934	101.22	0.0866	0.958
Humptulips	-1.250890	0.309214	105.36	2.5553	0.279
Simpson	-3.399604	0.915560	71.87	42.9540	<0.001
Willapa	-0.612706	0.019423	>200	4.3872	0.112
Lower Columbia River region:					
Grays River	-4.811502	1.121774	139.51	13.9650	<0.001
Elochomin	1.220424	-0.419391	28.51	0.4453	0.800
Cowlitz	-1.507804	0.313933	252.04	1.9533	0.377
Toutle River	-1.916084	0.431439	166.18	14.5020	<0.001
Washougal	-0.930568	0.093467	>200	6.9850	0.030

The results of the June SST and 48^o N cumulative upwelling quadratic models seem to agree with the hypothesis of optimal environmental conditions in upwelling areas put forth by Cury and Roy (1989). Using a yearly average of upwelling indices, Cury and Roy showed a “dome shaped” relationship between Pacific sardine (*Sardinops sagax cae-rulea*) recruitment and upwelling off the California coast, with upwelling units between

100 and 120 (m^3/sec per 100 miles of coastline) having the maximum recruitment. They concluded that there may be a optimal condition in the stable layers of the upper ocean for fish recruitment.

The reasoning behind the hypothesis has to do with the winds responsible for coastal upwelling. Upwelling indices are proportional to wind speed squared (Cury and Roy, 1989), with northerly along shore winds inducing upwelling and bringing nutrients into the coastal upwelling and enhancing primary production. However, high upwelling indices are also indicative of higher wind speeds. When wind speed becomes too high, wind mixing in the upper surface layer starts to take place, and starts to break up patches of phytoplankton (Demers et al., 1987). Huntsman and Barber (1977) showed that strong wind mixing in the upper water column layer produced by strong winds negatively affected zooplankton biomass and primary production. Cury and Roy (1989) suggested that turbulence as a result of wind mixing could limit recruitment in upwelling areas.

The upwelling measure used by Cury and Roy (1989) was a yearly average, while the quadratic model used here was based on a total of the monthly upwelling indices from March through September, and are therefore, not directly translatable to wind speeds. However, the cumulative upwelling covariates are derived from the monthly upwelling strength indices, so there is a relationship with upwelling strength, and therefore wind speed. Thus, it is possible that the quadratic model results also point to optimal conditions of salmon survival.

The June SST quadratic model results provide even stronger evidence of the presence of optimal conditions for salmon survival. Sea surface temperature is affected by upwelling bringing cooler water into the surface layer (Knauss, 1978), with increased upwelling reducing the effect of seasonal warming, and negatively correlated with SST (Schwing and Mendelssohn, 1997). Eleven hatcheries from two regions all show a maximum coho marine survival rate at June SST's of about 13 ^oC (mean of 13.45 ^oC). The SST-survival relationship shown here might indicate that as upwelling (and wind stress) becomes too strong, survival drops. However, higher June SST would indicate weaker upwelling conditions because some seasonal warming had taken place. The weaker upwelling conditions would have a detrimental effect on primary production, and hence food availability for young coho. Therefore, the optimal conditions for salmon survival would be at those upwelling and wind stress conditions corresponding to a June SST of around 13 ^{o}C. The quadratic relationship between June SST and survival adds support to the hypothesis of Cury and Roy (1989).

The negative correlation between survival to age two and the June monthly upwelling at 45^{o} N adds support to the optimal conditions and water column stability hypothesis. The upwelling indices are derived from wind velocities, as mentioned earlier. Therefore, the correlation between the strength of upwelling and survival may be more of a correlation with wind velocities and survival. The idea of lower survival with higher wind velocities would be consistent with the water column stability hypothesis (Cury and Roy, 1989). Additionally, there was a positive correlation with summer average SST and two-year old coho survival. The summer SST covariate is the average of the May-September monthly averages, which incorporated yearly the maximum SST for all the years in the analysis. Summer SST was negatively correlated with June upwelling at 45^{o} N (r = 0.4943), and the positive correlation between summer SST and survival would again be consistent with the water column stability hypothesis.

Gargett (1997) presented the idea of coastal water column stability being influenced by the strength of the winter Aleutian Low. In conditions of high water column stability, vertical movement is restricted which prevents the introduction of nutrients, but light conditions would be optimal for phytoplankton. When water column stability is low, nutrients are abundant, but vertical movement reduces the light levels required for phytoplankton growth. Off the coast of WA and OR, nutrient levels are the limiting factor for phytoplankton growth (Polovina et. al., 1995). Gargett proposed the existence of conditions in which upwelling is sufficient for nutrient input to the coastal waters, and yet having enough stability to maintain light levels. The argument of Gargett (1997) for the existence of optimal conditions was used primarily to explain the variation in production between northern (Alaskan) and southern (to Northern CA) stocks. However, the idea of optimal environmental conditions based on water column stability was similar to that presented by Cury and Roy (1989).

In the analysis of the CWT data, there was no significant relationship between the strength of the Aleutian Low pressure system as measured by the NPI and ocean survival to age two. However, much of the work associating Aleutian Low conditions and salmon production have been on a decadal scale (Beamish and Boullion, 1993; Francis and Hare, 1994). The NPI, a measure of the strength of the winter Aluetian Low is an averaged value, both spatially and temporally (Trenberth and Hurrell, 1994). However, the CWT data used in the analysis had a high annual variability, and the longest time series of CWT data from anyone hatchery was 19 years (Table 1). It is likely that because the NPI is averaged over both a region and over time, there may not be enough variability in the NPI on an annual scale to detect a relationship between survival and Aleutian Low strength with the annually variable CWT data over a short time series.

The other significant univariate model was the negative correlation between Northern Upwelling Extent and smolt survival. Again, the adverse affect of Northern Extent may be indicative of strong upwelling conditions that would induce wind mixing turbulence in the surface layer. The correlation between June 45^{o} N and Northern Upwelling Extent was 0.4865, which, while not high, does show some association. The correlation between NPI and Northern Extent was 0.5104, indicating weaker winter Aleutian Lows, and according to Gargett (1997), creating wind conditions more favorable to upwelling (lower NPI values indicate stronger winter Aleutian lows). Therefore, the negative association between Northern Extent and smolt survival might be another way of showing that very strong upwelling conditions, and hence strong wind stress has a detrimental effect on survival.

The bivariate model results were consistent with the same arguments already presented. Summer average SST has a positive association with survivorship in all models, and Northern Extent showed a predominantly negative association. However, the June SST and summer SST bivariate model presented a contradiction with a significant negative association between survivorship and June SST, even though June SST and summer SST were highly correlated (Table 2). This may be an artifact of the model since June SST is only represented as a linear covariate, although the data suggest a quadratic relationship. The sign of the June SST covariate changed when paired with Northern Extent, perhaps giving further evidence that weight should not be given to a strictly linear interpretation of the relationship between survivorship and June SST.

Management Implications

The quadratic relationships between survival and the oceanographic conditions of June SST and cumulative upwelling are also indicative of, and lead to the supposition of, optimal conditions for smolt survival. If optimal conditions do exist, then the view of what constitutes good ocean conditions for salmon survival would have to change. Particularly, it might not be wise to think only in terms of linear relationships with covariates, but realize that there might be a set or range of conditions that are beneficial for salmon survival. Figure 4.1 uses June SST to illustrate that ocean and climate conditions will vary from year to year, and that although there may be some periods of more constant conditions, it is also likely that one year may be optimal and the next year sub-optimal. A significant drop in survival was shown in Figure 3.13 for June SST less than around 12.5 ^{o}C and greater than 14 ^{o}C. In the period from 1972 to 1993, June SST was near 12 ^{o}C three times, and above 14 ^{o}C five times, indicating that years of poor survival occurr often enough that ocean conditions should perhaps be considered in management decisions.

Identifying adverse conditions for smolt survival could be an important tool for managing adults. The time span that ocean conditions are favorable (Figure 4.1) for smolt survival may not be that long (Matthews, 1984), and may vary yearly. Recognition that poor environmental conditions could reduce adult returns, and the ability to recognize those conditions would need to be part of management practices (Brodeur, 1993). Critical to management practices that take into account marine survival of smolts would be ability to separate out the aspects that cannot be controlled through human actions, such as ocean conditions, from those aspects that can be controlled by humans, such as harvest. Additional understanding of the influence of increased stock enhancement on adult returns during periods of poor smolt survival would also be valuable information, although it may be unlikely that hatcheries could respond quickly to year to year ocean condition variability.

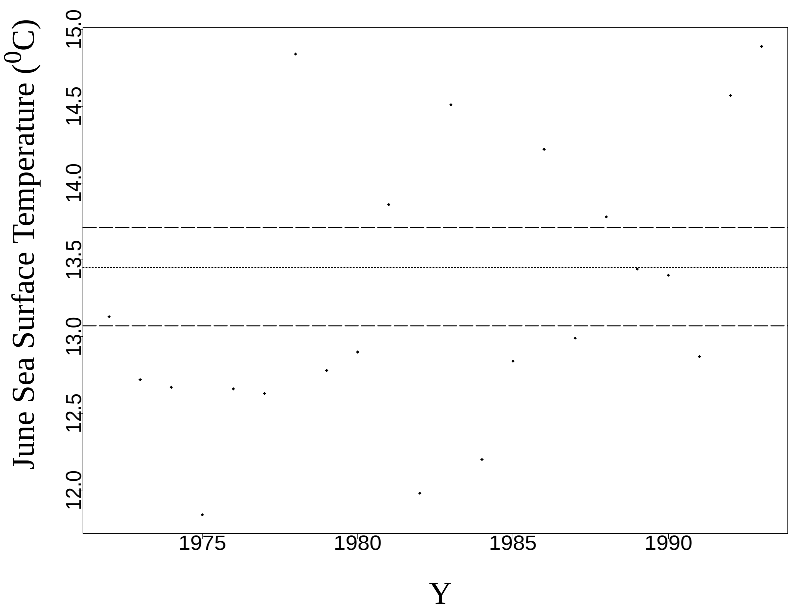

FIGURE 26. A time series plot of June sea surface temperature for the study period. Except for some years in the 1970's, the temperature varies widely from one year to the next, making it difficult to predict the next year's June temperature. The line going across the plot is the average maximum across all hatcheries, a value of 13.45 ^{o}C. The upper and lower lines represent the upper and lower limits (13.71 ^{o}C and 13.07 ^{o}C) of the range of maxima from the hatcheries.

Extension of methods to Chinook Salmon

The analysis presented in this thesis (Chapter 3) illustrated a new model for analyzing coho CWT return data, and a tractable method for obtaining survival and regression estimates. However, Columbia River chinook salmon are of primary interest to agencies managing resources on the river. The next step in developing this method is to extend the multinomial likelihood to the life history patterns of chinook salmon. Incorporating the slight differences between coho and chinook salmon ecology into the model is essential to understanding the relationship between chinook smolt survival and ocean environmental conditions. Even more important, is the question of whether enough years of data exist to estimate survival given the need for obtaining estimates from multiple hatcheries.

Chinook salmon return as adults at ages from two to seven. The additional age classes would need to be incorporated into the likelihood model (EQ 13), and would be given by

$$L(So, \beta_i, M_2, \theta_1, \theta_2, \theta_3, \theta_4, \theta_5 | R_i, t_{i2}, t_{i3}, t_{i4}, t_{i5}, t_{i6}, t_{i7}, x) =$$

$$\prod_{i=1}^{n} \binom{R}{\prod_{j=2}^{7} t_{ij}} (S_o^{e^{x'\beta}} M_{i2})^{t_{i2}} \bullet (S_o^{e^{x'\beta}} \theta_1)^{t_{i3}} \bullet (S_o^{e^{x'\beta}} (\theta_2))^{t_{i4}} \bullet$$

$$(S_o^{e^{x'\beta}} \theta_3)^{t_{i5}} \bullet (S_o^{e^{x'\beta}} \theta_4)^{t_{i6}} \bullet (S_o^{e^{x'\beta}} \theta_5)^{t_{i7}} \bullet$$

$$(1 - So^{e^{x'\beta}} (M_{i2} + \theta_1 + \theta_2 + \theta_3 + \theta_4 + \theta_5))^{R_i - \sum_{i=2}^{7} t_{ij}} , \quad \text{(EQ 21)}$$

where $S_o^{e^{x'\beta}}$ is the proportional hazards model estimating survival to age two, t_{i5}, t_{i6}, t_{i7} are the expanded tag recoveries from five, six and seven year old adult returns, and $\theta_3, \theta_4, \theta_5$ incorporate the probability of maturing and surviving at ages five, six and seven given survival to age two. The number of parameters in the univariate chinook model is eight, requiring at least nine or ten years of data for parameter estimation. Given that seven year old chinook salmon returning in 1997 would be from brood year 1990, and the time lag for CWT adult returns to enter the data base, the latest brood year that could be used in the analysis is probably 1989 (seven year olds returning in 1996).

There are some differences between chinook and coho with respect to marine residence patters, and some similarities between the two species. For example, one difference between the species is that chinook salmon are more dependent on estuaries than coho salmon, with yearling chinook being the most dependent on estuaries of all salmonid species (Pearcy, 1992). Similarities between the species include ocean entry at approximately the same time for chinook and coho salmon (Pearcy, 1992; Fisher and Pearcy, 1995), and would thus be exposed to similar ocean conditions early in marine residence. Fishes are the dominant food source for both species (Broduer et al., 1992), and the diets of both chinook and coho overlap (Brodeur and Pearcy, 1990). It would be reasonable to assume that chinook would be effected in the same ways as coho by changes in productivity in the coastal area, and both coho and yearling chinook appear to grow at the same rate (Fisher and Pearcy, 1995).

Chinook salmon exhibit within species differences with regard to where smolts are early in marine residence. Yearling (spring) and subyearling (fall) chinook salmon smolts inhabit different areas on the coast, with yearling chinook more offshore and sub-yearlings more inshore (Fisher and Pearcy, 1995). It also appears as though yearling chinook migrate north soon after ocean entry, while sub-yearling chinook are still near the WA coast in late summer. Separate analyses would be required for each of the different chinook types, to account for these differences between yearling and sub-yearling smolts. Due to similarities between yearling chinook and coho, some of the relationships between survival and environmental covariates found in coho may apply to yearling chinook, and the same model approach could be used for both species. However, due to the differences between yearling and sub-yearling chinook in location during early marine residence, migratory behavior, and the additional winter spent in the ocean by sub-yearlings to reach age two, the model may not be appropriate for sub-yearling chinook salmon.

Recommendations for future research

The results of the upwelling covariates hint at the importance of the timing of spring transition to salmon marine survival. The spring transition is when downwelling conditions present in the winter and early spring change to upwelling. The cumulative upwelling covariate would be correlated with spring transition, with early spring transitions yielding higher values of the covariate. Early spring transitions have a positive effect on primary and zooplankton production, and hence food production for smolts (Robinson, 1994). The salmon survival/cumulative upwelling, shows an increase in survivorship with an increase in cumulative upwelling to a maximum, then a decrease. This relationship, when taken into account with the negative correlation with June upwelling intensity, would point to the importance of prolonged, and not overly strong upwelling conditions being important to salmon survival, which again is an optimal set of environmental conditions.

For results showing the same effect for a covariate across the hatcheries within a region, a common regional β or S_o value could be estimated using the likelihood function,

$$L(S_o, \beta, M_{k2}, \theta_{k1}, \theta_{k2} | R_{ki}, t_{k2}, t_{k3}, t_{k4}, x_{ki}) =$$
$$\prod_{k=1}^{h}\left(\prod_{i=1}^{n}\left(\frac{R_{ki}}{\prod_{j=2}^{4} t_{ij}}\right)((S_o)^{e^{x'\beta}} M_{k2})^{t_{ki2}} \bullet ((S_o)^{e^{x'\beta}}\theta_{k1})^{t_{ki3}} \bullet ((S_o)^{e^{x'\beta}}(\theta_{k2}))^{t_{ki4}} \bullet \right.$$
$$\left.\left((1-(So)^{e^{x'\beta}}(M_{k2}+\theta_{k1}+\theta_{k2}))^{R_{ki}-\sum_{i=2}^{4} t_{kij}}\right)\right) . \quad \text{(EQ 22)}$$

where k indexes the different hatcheries in the region. The hypothesis H_o: $\beta = \beta_k$, for all k, versus H_a: $\beta \neq \beta_k$ was tested using a likelihood ratio test with k - 1 degrees of freedom. The regression coefficients could then be compared across regions.

The analysis of CWT data was focused on survival relationships with abiotic environmental ocean and climate factors. One biotic factor that may have an influence on marine smolt survival is the number of WA and OR hatchery releases leading to density dependent mortality. Many studies have looked into the presence of density dependent mortality in the early marine residence of salmon smolts, with many of the studies showing weak evidence for the presence of density dependance (Emlen, 1990; McGie, 1981; McCarl and Rettig, 1984; Lin and Williams, 1988). One study indicated that by the time hatchery smolts enter the ocean, they are above the size for density dependent effects (Holtby et. al., 1990), and another study suggested that environmental and ocean conditions would have a greater impact on smolt survival than density dependance (Nickelson, 1986). Two studies suggested an interaction between the number of smolts released into the ocean and environmental conditions limiting carrying capacity (McGie 1984, Beamish and Boullion 1993). It is this last point that should be looked into more closely, and perhaps as an interaction with non-linear effects already presented here.

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Appendix A

Coded Wire Tag Hatchery Data

Coded wire tag release and return data are present in the following tables by hatchery. Adult return numbers are expanded counts, and are present by both the brood year and year of ocean entry (outmigration). Some of the hatcheries have coho returning as five and even six years of age, however, the numbers were considered negligable and therefore were not modelled. The hatcheries are ordered by region.

Strait of Juan de Fuce Hatcheries:

Table A.1: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Dungeness Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers			
			2 yr old	3 yr old	4 yr old	5 yr old
70	72	54357	0.00	1344.40	0.00	0.00
71	73	9700	0.00	15.34	1.11	0.00
72	74	39746	0.00	1357.44	0.00	0.00
75	77	193648	38.49	10265.68	495.52	17.46
76	78	205375	77.78	13635.93	7.30	0.00
77	79	56311	27.14	4323.72	2.21	0.00
78	80	56857	9.81	3458.18	9.01	0.00
79	81	50607	42.65	4399.48	10.34	0.00
80	82	19843	5.85	616.69	0.00	0.00
83	85	196183	1.00	4279.52	0.00	0.00
86	88	201224	1.00	6685.90	0.00	0.00
89	91	10061	0.00	270.83	0.00	0.00
91	93	30488	0.00	368.00	0.00	0.00

Table A.2: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Lower Elwha Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
78	80	27868	91.85	409.73	4.00
79	81	28370	55.14	184.97	0.00
80	82	28410	38.57	150.05	0.00
81	83	27087	48.41	810.56	15.30
82	84	56252	46.46	2047.61	3.09
85	87	72340	0.00	178.73	0.00
86	88	203144	8.72	2633.48	2.00
87	89	60809	6.06	388.17	0.00
88	90	70405	1.00	122.28	0.00
89	91	69572	58.84	711.34	1.16
91	93	77287	89.00	233.00	0.00

Coastal Hatcheries:

Table A.3: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Soleduc Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers			
			2 yr old	3 yr old	4 yr old	5 yr old
71	73	83205	939.60	7195.68	0.00	0.00
72	74	74166	6.90	302.70	6.00	0.00
74	76	109459	1.00	844.89	0.00	4.00
75	77	285117	16.14	3000.49	0.00	0.00
76	78	152556	414.14	3562.60	0.00	0.00
80	82	154966	32.00	934.20	0.00	0.00
81	83	45121	208.09	2713.36	4.00	7.55
82	84	68971	17.68	331.59	0.00	0.00
83	85	92022	116.73	1919.80	0.00	0.00
84	86	220130	72.00	543.88	3.36	0.00
85	87	533018	586.97	4250.38	83.69	0.00
86	88	382901	583.70	3740.06	181.80	0.00
87	89	91893	152.32	490.78	9.08	0.00
88	90	283466	535.00	3247.46	315.61	0.00
90	92	72463	246.83	959.00	0.00	0.00
91	93	66026	5.00	558.00	0.00	0.00

Table A.4: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Quinault Lake Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers			
			2 yr old	3 yr old	4 yr old	5 yr old
77	79	61388	576.12	1161.65	0.00	0.00
78	80	132781	300.19	1557.59	14.10	0.00
79	81	78726	59.59	626.37	0.00	0.00
80	82	63631	8.90	802.89	1.00	0.00
81	83	103002	23.62	2459.46	5.69	0.00
82	84	110122	113.65	1410.67	0.00	0.00
83	85	194179	22.70	2159.20	2.65	0.00
84	86	106188	8.32	1593.96	0.00	0.00
85	87	82064	276.99	2473.61	0.00	4.54
86	88	77945	328.49	1791.33	0.00	1.00
88	90	41526	153.00	3021.00	0.00	0.00
89	91	150014	53.68	1504.00	7.68	0.00
90	92	228510	167.00	3981.99	3.07	0.00
91	93	121421	13.79	499.00	0.00	0.00

Table A.5: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Quinault National Fish Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
73	75	50253	0.00	760.18	0.00
74	76	150395	3.79	412.86	0.00
75	77	185970	4.00	1666.20	0.00
76	78	89934	52.71	2511.17	0.00
77	79	82260	466.12	2271.20	0.00
78	80	64000	104.91	1048.78	0.00
79	81	29096	34.04	158.39	0.00
80	82	33550	33.00	321.36	0.00
81	83	28526	9.00	662.09	0.00
82	84	25880	28.23	127.02	0.00
83	85	129115	194.69	1366.26	0.00
84	86	41201	12.10	590.62	0.00
85	87	77132	170.61	2018.36	0.00
86	88	76413	170.03	1177.19	0.00
87	89	71220	60.18	1311.20	0.00
88	90	70025	314.23	3673.93	0.00
89	91	78662	229.00	1406.79	0.00
90	92	68220	23.00	718.86	4.41
91	93	71325	0.00	43.00	0.00

Table A.6: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Humptulips Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
80	82	103300	6.36	1560.28	9.14
82	84	197437	3.00	881.03	0.00
83	85	391465	85.07	7336.41	2.43
84	86	112317	13.08	892.05	0.00
85	87	76714	247.05	4838.17	0.00
86	88	78760	191.79	3087.42	0.00
87	89	166083	118.36	3864.64	3.09
88	90	80082	80.99	4428.95	0.00
89	91	58287	5.30	598.28	1.85
90	92	77679	53.53	1157.89	0.00
91	93	124043	27.00	826.00	0.00

Table A.7: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Simpson Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
71	73	82415	9.20	2267.11	115.85
72	74	145688	13.38	1903.28	81.61
73	75	138394	4.83	3823.89	37.08
74	76	119789	0.00	608.49	8.00
75	77	84391	6.43	383.62	2.16
80	82	103903	4.10	969.90	46.14
81	83	84638	24.27	2791.13	164.09
82	84	95080	11.00	659.00	12.79
83	85	303285	21.02	1773.83	192.39
84	86	79315	8.00	1003.11	1.03
85	87	75862	61.29	1852.48	0.00
86	88	69421	8.64	2487.45	75.61
87	89	77071	21.61	2411.27	7.66
88	90	284741	137.51	6846.34	0.00
89	91	62288	26.78	2104.44	0.00
90	92	76053	29.00	1015.41	0.00
91	93	139543	1.05	385.00	10.00

Table A.8: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Willapa Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
71	73	60896	0.00	180.82	30.00
74	76	81742	17.00	450.72	0.00
80	82	50703	3.00	442.96	0.00
81	83	52796	20.20	2250.74	2.17
82	84	102492	26.17	1066.88	0.00
83	85	104311	32.15	7706.07	3.00
84	86	109599	1.46	2784.42	0.00
85	87	109178	83.01	4398.63	0.00
86	88	78499	656.60	3767.06	0.00

Lower Columbia River Hatcheries:

Table A.9: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Grays River Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
74	76	52082	0.00	16.30	0.00
75	77	51639	44.67	1120.42	0.00
76	78	47139	35.17	1157.16	0.00
77	79	101619	79.39	1309.86	4.89
78	80	208303	180.62	619.67	0.00
79	81	197453	289.24	4054.16	2.54
80	82	52110	139.87	239.16	0.00
81	83	50086	17.00	1134.27	0.00
82	84	48594	4.00	223.48	3.62
83	85	146660	125.74	3593.83	10.90
84	86	156888	12.00	792.67	2.49
85	87	157788	302.65	4406.65	5.73
88	90	32155	60.38	1120.85	0.00
89	91	31360	1.09	39.47	0.00
90	92	30385	0.00	10.07	0.00
91	93	60285	0.00	22.00	0.00

Table A.10: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Elochomin Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
72	74	72546	67.00	695.43	4.68
74	76	103517	27.68	1201.09	0.00
83	85	51767	14.00	1982.27	24.12
84	86	52497	22.00	326.25	0.00
85	87	52166	82.86	2216.17	0.00
88	90	30767	11.00	2462.84	0.00
89	91	50339	0.00	124.73	25.30
90	92	29890	1.00	105.38	0.00

Table A.11: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Cowlitz Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers				
			2 yr. old	3 yr. old	4 yr old	5 yr. old	6 yr. old
72	74	160055	686.90	4485.82	152.00	0.00	0.00
80	82	311011	868.95	5408.78	173.58	1.83	0.00
81	83	311009	984.12	5363.81	129.66	0.00	1.02
82	84	308343	192.50	3971.53	116.15	0.00	0.00
83	85	140444	654.35	7796.69	46.93	0.00	0.00
84	86	248383	544.17	4942.00	16.43	0.00	0.00
85	87	244684	1243.14	7540.16	43.98	0.00	0.00
86	88	155934	187.89	6499.23	81.98	0.00	0.00
87	89	90189	75.97	614.76	23.46	0.00	0.00
88	90	166581	447.46	7306.10	93.93	0.00	0.00
89	91	171670	189.05	1635.09	195.56	0.00	0.00

Table A.11: (continued)

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers				
			2 yr. old	3 yr. old	4 yr old	5 yr. old	6 yr. old
90	92	172485	188.52	811.47	136.44	0.00	0.00
91	93	71475	8.32	102.00	8.00	0.00	0.00

Table A.12: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Toutle River Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
72	74	435982	85.80	11138.29	17.98
77	79	238280	42.85	9984.19	2.14
78	80	78108	3.20	1018.74	0.00
86	88	49450	41.67	2488.00	0.00
87	89	49539	0.00	1784.75	0.00
88	90	49192	70.22	2478.28	0.00
89	91	30130	18.36	147.71	0.00
90	92	49365	20.00	692.00	0.00
91	93	197012	9.57	425.00	0.00

Table A.13: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Kalama Creek Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers			
			2 yr old	3 yr old	4 yr old	5 yr old
83	85	204454	59.13	14071.23	107.36	0.00
84	86	199614	23.69	2269.72	5.39	0.00
85	87	156053	211.64	9851.76	11.04	3.09
88	90	29973	10.00	2635.72	0.00	0.00
89	91	31237	0.00	210.55	0.00	0.00
90	92	30293	0.00	49.38	0.00	0.00
91	93	29999	0.00	33.00	0.00	0.00

Table A.14: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Kalama Falls Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers		
			2 yr old	3 yr old	4 yr old
77	79	10522	22.19	2184.85	2.30
85	87	48388	107.58	2873.43	0.00
86	88	50804	13.00	1035.22	3.01
87	89	50699	37.07	1395.57	0.00
88	90	50529	2.00	1138.00	0.00
89	91	50001	9.12	1617.71	2.00
91	93	49012	38.00	1128.00	0.00

Table A.15: A table showing the CWT release and return data by brood year and corresponding year of ocean entry for the Wahsougal Hatchery

Brood Year	Year of Ocean Entry	Number Released	Adult Returns - Expanded Numbers			
			2 yr old	3 yr old	4 yr old	5 yr old
74	76	47728	0.00	471.06	0.00	0.00
77	79	474021	79.41	16132.45	255.27	0.00
78	80	591840	34.58	31751.40	7.63	0.00
79	81	104679	18.15	4715.59	1.55	0.00
80	82	290487	43.25	2795.27	47.60	0.00
81	83	293034	1.20	1678.49	0.00	0.00
82	84	296897	96.07	5980.31	14.90	2.64
88	90	92005	5.00	2359.00	0.00	0.00
89	91	89303	7.26	1037.00	12.43	0.00
90	92	92152	0.00	104.28	9.00	0.00
91	93	91393	1.00	61.00	0.00	0.00

Appendix B

Ocean and Climate Covariate Values

Covariate values are presented in the following tables. The first column, observation year, in the year in which the ocean/ climate covariate values were observed, and the brood year is the cohort that was exposed to the covariate values in the year of outmigration. The two year difference in the brood year and observation year is because coho smolts outmigrating as yearlings in the spring, approximately 18 months after being spawned. The standardize and $\log_{10}$ values were used for the quadratic models.

Table B.1: A table showing Sea Surface Temperatures (SST) values used in the analysis. The standardized values were used for the quadratic models. The year of observation is the year in which the values were observed, and the brood year is the cohort whose first year of ocean life is the observation year.

Observation Year	Brood Year	June SST	Standardized June SST	Summer Average SST	Standardized Summer SST
72	70	13.13	-0.1445	12.716	-2.13521
73	71	12.72	-0.6004	13.768	-0.08300
74	72	12.67	-0.6560	13.590	-0.43023
75	73	11.84	-1.5787	12.964	-1.65142
76	74	12.66	-0.6671	13.414	-0.77357
77	75	12.63	-0.7004	13.190	-1.21054
78	76	14.84	1.7566	13.704	-0.20785
79	77	12.78	-0.5337	14.296	0.94701
80	78	12.90	-0.4002	13.720	-0.17663
81	79	13.86	0.6671	14.162	0.68561
82	80	11.98	-1.4231	13.284	-1.02717
83	81	14.51	1.3897	14.596	1.53224
84	82	12.20	-1.1785	13.550	-0.50825

Table B.1: (continued)

Observation Year	Brood Year	June SST	Standardized June SST	Summer Average SST	Standardized Summer SST
85	83	12.84	-0.4670	13.702	-0.21175
86	84	14.22	1.0673	13.966	0.30326
87	85	12.99	-0.3002	13.922	0.21742
88	86	13.78	0.5781	13.808	-0.00497
89	87	13.44	0.2001	14.372	1.09527
90	88	13.40	0.1557	14.654	1.64539
91	89	12.87	-0.4336	13.754	-0.11031
92	90	14.57	1.4564	14.420	1.18891
93	91	14.89	1.8122	14.280	0.91580

Table B.2: A table showing the Northwest Pacific Index (NPI) and Pacific Northwest Index (PNI) values used in the analysis. The year of observation is the year in which the values were observed, and the brood year is the cohort whose first year of ocean life is the observation year.

Observation Year	Brood Year	NPI values	PNI values
72	70	2.45	-1.39
73	71	0.13	0.33
74	72	-0.32	-1.08
75	73	0.64	-0.84
76	74	0.71	-0.05
77	75	-3.43	0.85
78	76	-2.89	0.89
79	77	1.17	0.43
80	78	-1.70	0.44
81	79	-4.95	1.16
82	80	1.22	-0.25
83	81	-5.92	0.68
84	82	-3.10	0.52
85	83	0.62	0.75
86	84	-4.59	0.33
87	85	-3.42	1.06
88	86	-1.25	0.44
89	87	2.36	0.35
90	88	1.52	-1.10
91	89	1.86	0.11
92	90	-2.93	1.42
93	91	-0.64	1.03

Table B.3: A table showing the Bakun index values for coastal upwelling at 45^{o} North used in the analysis. The year of observation is the year in which the values were observed, and the brood year is the cohort whose first year of ocean life is the observation year.

Observation Year	Brood Year	45 N June	Standardized 45 N June	45 N Summer Average
72	70	55	0.4270	43.2
73	71	27	-0.7236	46.8
74	72	80	1.4544	46.0
75	73	98	2.1941	54.0
76	74	56	0.4681	26.2
77	75	71	1.0845	40.2
78	76	34	-0.4360	32.4
79	77	86	1.7009	36.2
80	78	32	-0.5181	58.4
81	79	8	-1.5044	33.2
82	80	59	0.5914	47.8
83	81	19	-1.0524	26.4
84	82	37	-0.3127	39.2
85	83	52	0.3037	41.6
86	84	25	-0.8058	37.2
87	85	43	-0.0661	43.4
88	86	14	-1.2578	32.4
89	87	43	-0.0661	41.4
90	88	15	-1.2167	37.2
91	89	59	0.5914	54.8
92	90	61	0.6736	57.4
93	91	24	-0.8469	38.2

Table B.4: A table showing the Bakun index values for coastal upwelling at 48^o North used in the analysis, and the values for Northern upwelling extent. The year of observation is the year in which the values were observed, and the brood year is the cohort whose first year of ocean life is the observation year.

Observation Year	Brood Year	48 N June	48 N Summer Average	Northern Upwelling Extent
72	70	27	17.6	3
73	71	11	21.2	1
74	72	38	22.0	3
75	73	59	28.6	2
76	74	31	10.4	2
77	75	39	23.2	2
78	76	28	18.0	3
79	77	83	33.0	2
80	78	32	41.8	2
81	79	5	22.2	1
82	80	74	42.8	3
83	81	24	25.0	1
84	82	33	26.2	1
85	83	49	39.8	2
86	84	26	35.6	2
87	85	37	35.0	1
88	86	12	26.0	1
89	87	31	33.0	3
90	88	12	23.6	2
91	89	31	22.2	3
92	90	42	32.0	3
93	91	23	21.0	2

Table B.5: Table showing the cumulative upwelling index values at 45^o and 48^o North for the period from March to September, inclusive. The year of observation is the year in which the values were observed, and the brood year is the cohort whose first year of ocean life is the observation year.

Observation Year	Brood Year	45 N Upwelling	48 N Upwelling	Log_{10} 48 N Upwelling
72	70	190	51	1.7076
73	71	276	122	2.0864
74	72	195	76	1.8808
75	73	304	156	2.1931
76	74	121	25	1.3979
77	75	210	125	2.0969
78	76	160	83	1.9191
79	77	187	173	2.2380
80	78	286	197	2.2945
81	79	152	94	1.9731
82	80	232	213	2.3284
83	81	40	67	1.8261
84	82	155	88	1.9445
85	83	208	197	2.2945
86	84	163	132	2.1206
87	85	178	133	2.1239
88	86	153	119	2.0755
89	87	149	93	1.9685
90	88	193	113	2.0531
91	89	282	112	2.0492
92	90	280	152	2.1818
93	91	92	11	1.0414

Appendix C

Univariate model results

Presented in the following tables are the estimated coefficients of the univariate model for each hatchery, the adjusted standard errors of the estimates, and the baseline survival S_o. Adjusted standard errors were derived by multiplying the standard error estimated from the data by the square root of the scale parameter (Equations 10 & 11). The reason for the adjustment is to attempt to account for year to year variability. Both the coefficient values and the standard error estimates were used in the weighted t-test of the regional and overall means.

Table C.1: Parameter estimates for the univariate proportional hazards (PH) models with Sea Surface Temperature (SST) as the covariate. The univariate model is $(So)^{e^{\beta \bullet (SST)}}$, and models survival to age two

Hatchery	June Temperature			Summer Temperature		
	S_o	β	SE(β)	S_o	β	SE(β)
Strait of Juan de Fuca Region						
Dungeness	0.00284	-0.04749	0.03112	0.000284	-0.07113	0.07557
Lower Elwha	0.14919	0.064775	0.0531	0.78901	0.211382	0.11005
Coastal Region						
Soleduc	0.002150	-0.02561	0.05509	$1.81\ 10^{-5}$	-0.0661	0.1004
Quinault Lake	0.01985	0.00385	0.12687	$1.11\ 10^{-19}$	-.016808	0.05855
Quinault National Fish	0.003001	-0.02517	0.03092	$3.17\ 10^{-31}$	-0.20380	0.35929
Humptulips	0.01557	-0.00479	0.04714	$3.83\ 10^{-22}$	-0.18184	0.04487
Simpson	0.005414	-0.02033	0.02727	$8.25\ 10^{-30}$	-0.20366	0.04882
Willapa	0.000001	-0.10234	0.07149	$1.15\ 10^{-66}$	-0.27348	0.17169

Table C.1: (continued)

Hatchery	June Temperature			Summer Temperature		
	S_o	β	SE(β)	S_o	β	SE(β)
Lower Columbia Region						
Grays River	0.018807	0.00469	0.03204	$2.42\ 10^{-8}$	-0.10136	0.07786
Elochomin	0.103537	0.04113	0.11076	$3.3\ 10^{-148}$	-0.32273	0.31619
Cowlitz	0.063886	0.02458	0.03106	0.035432	0.009457	0.06050
Toutle River	0.57625	0.144088	0.00775	$8.07\ 10^{-4}$	-0.04733	0.05391
Kalama Creek	0.74666	0.180451	0.09167	0.18814	0.048281	0.22474
Kalama Falls	0.97501	0.363109	0.05624	0.90091	0.244924	0.23973
Washougal	0.171565	0.054404	0.05155	0.27897	0.074434	0.08521

Table C.2: Parameter estimates for the univarite proportional hazards (PH) models with one of the two yearly climate indices, NPI or PNI, as the covariate. The univariate model is $(So)e^{\beta \bullet (Index)}$, and models survival to age two.

Hatchery	North Pacific Index (NPI)			Pacific Northwest Index (PNI)		
	S_o	β	SE(β)	S_o	β	SE(β)
Strait of Juan de Fuca						
Dungeness	0.034836	0.05253	0.01225	0.037535	-0.10365	0.04638
Lower Elwha	0.008706	0.03865	0.01387	0.009724	-0.05877	0.07163
Coastal:						
Soleduc	0.013523	-0.00873	0.01931	0.012373	-0.01553	0.06217
Quinault Lake	0.015982	0.001189	0.01304	0.020798	0.102439	0.04629
Quinault National Fish	0.016424	-0.01352	0.01112	0.018490	0.101648	0.0360
Humptulips	0.020606	-0.01421	0.01865	0.023274	0.081938	0.06564
Simpson	0.019026	-0.01494	0.01674	0.019892	0.136349	0.04146
Willapa	0.030839	-0.00056	0.01646	0.012610	-0.41890	0.13736
Lower Columbia						
Grays River	0.012467	0.011448	0.01148	0.009998	-0.11191	0.06114
Elochomin	0.021126	-0.01282	0.02826	0.020626	0.010993	0.07434
Cowlitz	0.023572	-0.01052	0.56945	0.023559	0.058797	0.03924
Toutle River	0.027098	-0.06196	0.02562	0.027177	0.029790	0.04030
Kalama Creek	0.036795	0.018872	0.03513	0.032392	-0.09647	0.10405
Kalama Falls	0.054461	-0.04880	0.02123	0.040336	-0.02838	0.10616
Washougal	0.028271	-0.00832	0.01537	0.026891	-0.00856	0.08122

Table C.3: Parameter estimates for the univarite proportional hazards (PH) models with one of the two measurements of upwelling conditions at 45^{o} N, June or Summer average, as the covariate. The univariate model is $(So)^{e^{\beta \bullet (45NUp)}}$, and models survival to age two.

Hatchery	45^{o} North June Upwelling			45^{o} North Summer Upwelling		
	S_o	β	SE(β)	S_o	β	SE(β)
Strait of Juan de Fuca						
Dungeness	0.043611	-0.00029	0.00127	0.079391	0.005196	0.00406
Lower Elwha	0.011239	0.00023	0.1043	0.019024	0.00336	0.00474
Coastal:						
Soleduc	0.019427	0.002759	0.00213	0.010532	-0.00108	0.00635
Quinault Lake	0.018776	0.000935	0.00154	0.028117	0.003332	0.00298
Quinault National Fish	0.021292	0.001633	0.00108	0.013248	-0.00097	0.00292
Humptulips	0.031729	0.003085	0.00246	0.044130	0.00541	0.00711
Simpson	0.030675	0.002919	0.00142	0.019238	$-2\ 10^{--6}$	0.00014
Willapa	0.035950	0.001250	0.00353	0.030517	$-5.2\ 10^{-5}$	0.00438
Lower Columbia						
Grays River	0.015159	0.000518	0.00125	0.044831	0.007938	0.00316
Elochomin	0.066232	0.007392	0.00248	0.035222	0.003717	0.00666
Cowlitz	0.026382	0.001184	0.00142	0.045360	0.005124	0.00337
Toutle River	0.015312	-0.00211	0.00139	0.097688	0.010720	0.00435
Kalama Creek	0.010545	-0.00836	0.24539	0.029926	-0.00146	0.01036
Kalama Falls	Did not converge			0.051129	0.001408	0.01201
Washougal	0.028123	0.000199	0.00142	0.005209	-0.00844	0.00281

Table C.4: Parameter estimates for the univarite proportional hazards (PH) models with one of the two measurements of upwelling conditions at 48^{o} N, June or Summer average, as the covariate. The univariate model is $(So)^{e^{\beta \bullet (48NUp)}}$, and models survival to age two.

Hatchery	48^{o} North June Upwelling			48^{o} North Summer Upwelling		
	S_o	β	SE(β)	S_o	β	SE(β)
Strait of Juan de Fuca						
Dungeness	0.044655	-0.00016	0.00144	0.07480	0.006653	0.00324
Lower Elwha	0.010336	-0.00049	0.00267	0.014230	0.002219	0.00660
Coastal:						
Soleduc	0.023266	0.005229	0.00257	0.035228	0.009625	0.00506
Quinault Lake	0.017893	0.000744	0.00176	0.014108	-0.0010	0.00392
Quinault National Fish	0.016055	0.000178	0.00127	0.009418	-0.00417	0.00308
Humptulips	0.030568	0.003171	0.0024	0.018359	-0.00070	0.00554
Simpson	0.040516	0.006413	0.00201	0.029025	0.004337	0.00455
Willapa	0.026055	-0.00140	0.00332	Did not converge		
Lower Columbia						
Grays River	0.015403	0.000698	0.00134	0.017914	0.001954	0.00312
Elochomin	0.036572	0.004839	0.0079	0.008060	-0.00813	0.00595
Cowlitz	0.025647	0.001135	0.00163	0.015351	-0.00300	0.00389
Toutle River	0.015533	-0.00293	0.00148	0.010959	-0.00775	0.00532
Kalama Creek	0.008385	-0.01259	0.00119	0.001984	-0.02279	0.01003
Kalama Falls	0.009411	-0.01061	0.00539	0.002840	-0.01757	0.01173
Washougal	0.028285	0.000240	0.00145	Did not converge		

Table C.5: Parameter estimates for the univarite proportional hazards (PH) models with the March - September cumulative upwelling indices for 45° N or 48° N as the covariate. The univariate model is $(So)^{e^{\beta \bullet (Totalup)}}$, and models survival to age two. Also included are the adjusted standard errors of the regression coefficients, β.

Hatchery	45° Cumulative Upwelling			48° Cumulative Upwelling		
	S_o	β	SE(β)	S_o	β	SE(β)
Strait of Juan de Fuca						
Dungeness	0.06051	0.04237	0.30813	0.041517	-0.01378	0.1156
Lower Elwha	0.059821	0.216225	0.20124	0.004754	-0.08581	0.13214
Coastal:						
Soleduc	0.01023	-0.02191	0.26654	0.01269	-0.00137	0.03603
Quinault Lake	0.023538	0.042627	0.13826	0.003824	-0.14488	0.14428
Quinault National Fish	0.001563	-0.19514	0.17243	$3.48\ 10^{-4}$	-0.31942	0.08796
Humptulips	$9.9\ 10^{-4}$	-0.25344	0.3536	0.003437	-0.18013	0.13874
Simpson	0.014287	-0.01509	0.20057	0.003642	-0.15542	0.08546
Willapa	0.044519	0.051275	0.26982	$2.48\ 10^{-5}$	-0.53825	0.22661
Lower Columbia						
Grays River	0.053282	0.168205	0.15427	0.002809	-0.15300	0.11302
Elochomin	0.020515	-0.00021	0.00710	$8.9\ 10^{-4}$	-0.30132	0.01940
Cowlitz	0.013166	-0.05807	0.02669	0.001043	-0.28585	0.13604
Toutle River	$8.03\ 10^{-6}$	-0.51560	0.28262	$2.47\ 10^{-4}$	-0.41838	0.08503
Kalama Creek	$8.58\ 10^{-4}$	-0.34068	0.13048	0.005584	-0.23283	0.18351
Kalama Falls	$5.58\ 10^{-11}$	-0.88528	0.67811	$1.57\ 10^{-11}$	-0.95399	0.51379
Washougal	$1.36\ 10^{-6}$	-0.57986	0.14325	$6.36\ 10^{-6}$	-0.56062	0.18279

Table C.6: Parameter estimates for the univarite proportional hazards (PH) models with Northern Upwelling Extent as the covariate. The univariate model is $(So)^{e^{\beta \bullet (NorExnt)}}$, and models survival to age two. Also included are the adjusted standard errors of the regression coefficients, β.

Hatchery	Northern Upwelling Extent		
	S_o	β	SE(β)
Strait of Juan de Fuca			
Dungeness	0.03565	-0.03611	0.03819
Lower Elwha	0.019701	0.088511	0.04529
Coastal:			
Soleduc	0.019277	0.057495	0.0537
Quinault Lake	0.022836	0.045226	0.04074
Quinault National Fish	0.014546	-0.00829	0.03794
Humptulips	0.028679	0.047691	0.0513
Simpson	0.025700	0.043803	0.05399
Willapa	0.035155	0.026013	0.08746
Lower Columbia			
Grays River	0.032325	0.127919	0.04387
Elochomin	0.093605	0.237097	0.08587
Cowlitz	0.030193	0.044562	0.03248
Toutle River	0.039068	0.050640	0.05602
Kalama Creek	0.047786	0.042210	0.08868
Kalama Falls	0.119200	0.219715	0.10339
Washougal	0.031866	0.023525	0.05655

Appendix D

Quadratic model results by hatchery

The tables presented here show the estimated regression coefficients for the quadratic PH model for all of the hatcheries. The standard errors (se) are the adjusted standard errors that were used in the weighted t-test. Adjusted standard errors were derived by multiplying the standard error estimated from the data by the square root of the scale parameter (Equations 10 & 11) in an attempt to account for year to year variability. The first column, S_o is the baseline survival estimate.

Table D.1: Results of the quadratic model of June monthly Sea Surface Temperature (SST). The quadratic PH model is $(S_o)^{e^{\beta_1 JunSST + \beta_2 (JunSST)^2}}$, and models survival to age two.

Hatchery	June Quadratic				
	S_o	Linear Term - $\hat{\beta}_1$	se($\hat{\beta}_1$)	Quadratic Term - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.039894	-0.002511	0.02834	-0.040498	0.02979
Lower Elwha	0.009707	0.075330	0.04088	-0.046959	0.03661
Coastal:					
Soleduc	0.012024	-0.014101	0.06127	0.014969	0.05611
Quinault Lake	0.02116	-0.050436	0.03940	0.082015	0.03867
Quinault National Fish	0.019788	-0.071734	0.03502	0.071797	0.03089
Humptulips	0.030324	-0.059735	0.04056	0.150492	0.03779
Simpson	0.018740	-0.016887	0.02741	0.034113	0.02550
Willapa	0.048477	-0.128679	0.05639	0.187913	0.07471
Lower Columbia					

Table D.1: (continued)

Hatchery	June Quadratic				
	S_o	Linear Term - $\hat{\beta}_1$	se($\hat{\beta}_1$)	Quadratic Term - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Grays River	0.018143	-0.05827	0.004353	0.009934	0.004321
Elochomin	0.059584	-0.28411	0.08104	0.663607	0.11912
Cowlitz	0.033165	0.003800	0.02122	0.117797	0.01668
Toutle River	0.044513	-0.083449	0.04836	0.236840	0.04528
Washougal	0.045359	0.046526	0.01486	0.230626	0.02396

Table D.2: Results of the quadratic model of Summer average Sea Surface Temperature (SST). The quadratic PH model is $(S_o)^{e^{\beta_1 SumSST + \beta_2 (SumSST)^2}}$, and models survival to age two.

Hatchery	Summer Quadratic				
	S_o	Linear Term - $\hat{\beta}_1$	se($\hat{\beta}_1$)	Quadratic Term - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.047769	-0.102704	0.05758	0.004045	0.03929
Lower Elwha	0.011482	0.152507	0.07755	-0.051345	0.06639
Coastal:					
Soleduc	0.012963	-0.041844	0.06019	0.013717	0.05296
Quinault Lake	0.012368	-0.012206	0.05879	-0.078717	0.05196
Quinault National Fish	0.013775	-0.097721	0.02390	-0.022444	0.02447
Humptulips	0.017966	-0.085025	0.07337	-0.010341	0.06700
Simpson	0.013031	-0.028528	0.0245	-0.045280	0.02329
Willapa	0.036887	-0.239649	0.10517	0.158705	0.09263
Lower Columbia					
Grays River	0.012839	-0.04295	0.04563	-0.01802	0.04416
Elochomin	0.017550	-0.12026	0.10016	-0.05128	0.08742
Cowlitz	0.023222	-0.00998	0.04492	0.019040	0.04158
Toutle River	0.020406	0.079059	0.09987	-0.13672	0.11092
Washougal	0.044954	-0.125843	0.04982	0.261678	0.05349

Table D.3: Results of the quadratic model of June upwelling at 45^o N. The quadratic PH model is $(S_o)e^{\beta_1 Jun45 + \beta_2 (Jun45)^2}$, and models survival to age two.

Hatchery	45^o N June Upwelling Quadratic				
	S_o	Linear Term - $\hat{\beta}_1$	se($\hat{\beta}_1$)	Quadratic Term - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.038583	-0.001994	0.02426	-0.053644	0.03202
Lower Elwha	0.012041	0.097144	0.10922	0.100180	0.10111
Coastal:					
Soleduc	0.012944	0.080202	0.05685	0.040871	0.06909
Quinault Lake	0.013325	0.012459	0.03390	-0.059177	0.03771
Quinault National Fish	0.012975	0.062125	0.02594	-0.053883	0.02267
Humptulips	0.016375	-0.006131	0.09424	-0.037962	0.12054
Simpson	0.011614	0.071344	0.02417	-0.072465	0.02002
Willapa	0.02622	-0.066451	0.15037	-0.136665	0.17693
Lower Columbia					
Grays River	0.012533	0.010063	0.33055	-0.025245	0.02920
Elochomin	0.021932	0.180729	0.06133	-0.019266	0.06820
Cowlitz	0.018304	0.018957	0.03502	-0.064486	0.04418
Toutle River	0.008379	0.051016	0.04394	-0.164687	0.05477
Washougal	0.024066	0.024183	0.04375	-0.032606	0.04184

Table D.4: Results of the quadratic model of March - September cumulative upwelling at 48^{o} N. The quadratic PH model is $(S_o)e^{\beta_1 Cu(48) + \beta_2 (Cu48)^2}$, and models survival to age two.

Hatchery	48^{o} N Cumulative Upwelling Quadratic				
	S_o	Linear Term - $\hat{\beta}_1$	se($\hat{\beta}_1$)	Quadratic Term - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	$3.12\ 10^{-16}$	-2.682847	1.5692	0.718690	0.4116
Lower Elwha	$1.58\ 10^{-15}$	-2.563124	1.5692	0.764337	0.4742
Coastal:					
Soleduc	$4.83\ 10^{-9}$	-1.763185	1.7701	0.503549	0.49940
Quinault Lake	$3.33\ 10^{-11}$	-1.936352	0.88629	0.514513	0.24923
Quinault National Fish	$1.81\ 10^{-88}$	-3.934106	18.3963	0.980934	4.85543
Humptulips	$1.39\ 10^{-6}$	-1.250890	1.03635	0.309214	0.29508
Simpson	$6.10\ 10^{-39}$	-3.399604	0.72708	0.915560	0.19935
Willapa	$1.15\ 10^{-5}$	-0.612706	2.02757	0.019423	0.52536
Lower Columbia					
Grays River	$1.9\ 10^{-201}$	-4.811502	1.84164	1.121774	0.45575
Elochomin	0.015715	1.220424	2.92666	-0.419391	0.80498
Cowlitz	$2.27\ 10^{-10}$	-1.507804	1.40261	0.313933	0.35150
Toutle River	$3.73\ 10^{-13}$	-1.916084	0.64473	0.431439	0.18120
Washougal	$3.60\ 10^{-8}$	-0.930568	0.41209	0.093467	0.06807

Appendix E

Bivariate regression coefficients by hatchery

The tables in this appendix provide the regression coefficient estimates, the adjusted standard errors of the estimates, and the baseline survival S_o for the fitted bivariate model. The form of the bivariate proportional hazards (PH) models are given in the table captions. Since a minimum of eight years of data were needed to estimate the parameters in the bivariate model, there were only 13 hatcheries used in the analysis, since two of the fifteen hatcheries had only seven years worth of data.

Table E.1: Results of the bivariate model with Summer average SST and June SST for all hatcheries. The bivariate PH model is $(S_o)^{e^{\beta_1 SumSST + \beta_2 JunSST}}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	June SST				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	June SST - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000001	-0.068536	0.078981	-0.054762	0.033110
Lower Elwha	0.722199	0.218396	0.146900	-0.032204	0.076120
Coastal:					
Soleduc	0.000004	-0.179650	0.091020	0.060031	0.093970
Quinault Lake	0.000001	-0.140595	0.099540	0.015223	0.010394
Quinault National Fish	0.000001	-0.151665	0.126130	0.025689	0.132520
Humptulips	0.000001	-0.111785	0.035370	0.000572	0.016190
Simpson	0.000001	-0.060686	0.120020	-0.073906	0.125520

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Table E.1: (continued)

Hatchery	SUMMER Sea Surface Temperature (SST)				
	June SST				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	June SST - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Willapa	0.000001	-0.152032	0.290230	0.015270	0.015270
Lower Columbia					
Grays River	0.000001	-0.060807	0.109110	0.036162	0.036162
Elochomin	0.000001	-0.203749	0.339380	0.060070	0.060070
Cowlitz	0.004205	-0.037962	0.051340	0.071553	0.071553
Toutle River	0.000001	-0.068536	0.078981	-0.054762	0.033110
Washougal	0.091120	0.218396	0.146900	-0.032204	0.076120

Table E.2: Results of the bivariate model with Summer average SST and North Pacific Index (NPI) for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 SumSST + \beta_2 NPI}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	North Pacific Index (NPI)				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	NPI - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000001	-0.121033	0.042776	0.052122	0.012350
Lower Elwha	0.712819	0.188534	0.089490	0.037861	0.013220
Coastal:					
Soleduc	0.000021	-0.123953	0.011600	-0.008756	0.022850
Quinault Lake	0.000001	-0.123752	0.009980	-0.009985	0.019440
Quinault National Fish	0.000001	-0.126205	0.017680	0.009364	0.027900
Humptulips	0.000001	-0.111133	0.036810	-0.003655	0.012370
Simpson	0.000001	-0.137581	0.018960	-0.014640	0.032740
Willapa	0.000001	-0.111236	-0.111236	0.004085	0.004085
Lower Columbia					
Grays River	0.000001	-0.030309	-0.030309	-0.013141	-0.013141
Elochomin	0.000001	-0.114034	-0.114034	-0.031274	-0.031274
Cowlitz	0.003510	-0.121033	0.042776	0.052122	0.012350
Toutle River	0.000001	0.188534	0.089490	0.037861	0.013220
Washougal	1.000*	-0.06226*	*	-4.8364*	*

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient averages.

Table E.3: Results of the bivariate model with Summer average SST and the Pacific Northwest Index (PNI) for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 SumSST + \beta_2 PNI}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	Pacific Northwest Index (PNI)				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	**PNI** - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.001098	-0.054085	0.077600	-0.104080	0.049180
Lower Elwha	0.598663	0.157508	0.109120	-0.091166	0.081880
Coastal:					
Soleduc	0.000001	-0.096942	0.105150	-0.039363	0.063810
Quinault Lake	0.000001	-0.127222	0.011100	0.103102	0.095320
Quinault National Fish	0.000001	-0.125166	0.010270	0.075913	0.070070
Humptulips	0.000001	-0.127384	0.176500	0.038135	0.106710
Simpson	0.000001	-0.106927	0.045270	0.039319	0.030060
Willapa	0.000001	-0.084086	0.272460	-0.388556	0.243190
Lower Columbia					
Grays River	0.000001	-0.130444	-0.130444	-0.125279	-0.125279
Elochomin	0.000001	-0.128503	-0.128503	0.009022	0.009022
Cowlitz	0.011842	-0.012379	-0.012379	0.050403	0.050403
Toutle River	0.000001	-0.130684	-0.130684	0.021074	0.021074
Washougal	0.257409	0.070991	0.070991	-0.058422	-0.058422

Table E.4: Results of the bivariate model with Summer average SST and June Upwelling at 45° N for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 SumSST + \beta_2 June45up}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	45° N June Upwelling				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	45° N June - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000001	-0.130940	0.110380	-0.000787	0.001630
Lower Elwha	0.812808	0.215656	0.122490	0.002099	0.002510
Coastal:					
Soleduc	0.977301	0.977301*	0.124378*	*	0.029700*
Quinault Lake	0.000001	-0.124614	0.016680	0.001436	0.046290
Quinault National Fish	0.000001	-0.127913	0.011130	0.001190	0.001980
Humptulips	0.000001	-0.133877	0.027980	0.003392	0.003830
Simpson	0.000001	-0.110214	0.027120	0.000008	0.003760
Willapa	0.000001	-0.134542	0.021390	-0.000283	0.004880
Lower Columbia					
Grays River	0.000001	-0.115045	-0.115045	0.000214	0.000214
Elochomin	0.000001	-0.147162	-0.147162	0.005266	0.005266
Cowlitz	0.193264	0.053521	0.053521	0.002195	0.002195
Toutle River	0.000001	-0.130366	-0.130366	0.000102	0.000102
Washougal	0.193742	0.053989	0.053989	0.000524	0.000524

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient averages

Table E.5: Results of the bivariate model with Summer average SST and the average summer upwelling conditions at 45° N for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 SumSST + \beta_2 Sum45up}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	45° N Summer Upwelling				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	45° N Summer - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000157	-0.087478	0.082710	0.003794	0.004240
Lower Elwha	0.878204	0.234743	0.115828	0.006734	0.004720
Coastal:					
Soleduc	0.000001	-0.155531	0.224450	-0.002990	0.013030
Quinault Lake	0.000001	-0.131213	0.020700	0.003462	0.004830
Quinault National Fish	0.000001	-0.123314	0.012040	-0.000074	0.002210
Humptulips	0.000001	-0.126071	0.185360	0.000011	0.000550
Simpson	0.000001	-0.109670	0.020410	-0.003546	0.004850
Willapa	0.000001	-0.129187	0.031810	-0.001300	0.009990
Lower Columbia					
Grays River	0.000227	-0.069906	0.079370	0.007151	0.003280
Elochomin	0.000001	-0.151684	0.036130	0.007096	0.010118
Cowlitz	0.998699*	-0.81283*	*	0.325925*	*
Toutle River	0.207763*	-0.07933*	*	0.028424*	*
Washougal	0.000001	-0.093009	0.140290	-0.009813	0.005120

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient averages

Table E.6: Results of the bivariate model with Summer average SST and June Upwelling at 48° N for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 SumSST + \beta_2 June48up}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	48° N June Upwelling				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	48° N June - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000001	-0.110768	0.078400	0.000077	-0.110768
Lower Elwha	0.798710	0.211240	0.130650	0.001721	0.211240
Coastal:					
Soleduc	0.061911	0.020795	0.010185	0.005588	0.002990
Quinault Lake	0.000001	-0.122740	0.018180	0.000884	0.002870
Quinault National Fish	0.000001	-0.124452	0.011800	0.000290	0.002480
Humptulips	0.000001	-0.130301	0.030550	0.002349	0.005300
Simpson	0.001278	0.043312	0.058550	0.003092	0.001830
Willapa	0.000001	-0.128747	0.022100	-0.002380	0.004510
Lower Columbia					
Grays River	0.000001	-0.113112	0.027680	0.000509	0.001800
Elochomin	0.000001	-0.133973	0.024060	0.002716	0.007450
Cowlitz	0.218786	0.059418	0.084720	0.002414	0.002167
Toutle River	0.000001	-0.159503	0.370610	-0.000359	0.012810
Washougal	0.205156	0.056292	0.645600	0.000615	0.420850

Table E.7: Results of the bivariate model with Summer average SST and the average summer upwelling conditions at 48° N for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 SumSST + \beta_2 Sum48up}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	48° N Summer Upwelling				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	48° N Summer - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000001	-0.153189	0.04326	0.008950	0.00476
Lower Elwha	0.848253	0.217982	0.11816	0.009314	0.00726
Coastal:					
Soleduc	0.000019	-0.087085	0.09092	0.010660	0.00531
Quinault Lake	0.000001	-0.124701	0.02599	0.002352	0.00765
Quinault National Fish	0.000001	-0.120961	0.01450	-0.001257	0.00542
Humptulips	0.000001	-0.125335	0.17312	0.000135	0.00074
Simpson	0.000001	-0.107089	0.04006	0.003667	0.00291
Willapa	0.000001	-0.106566	0.02430	-0.013764	0.00958
Lower Columbia					
Grays River	0.000001	-0.114823	0.02815	0.002530	0.00386
Elochomin	0.000001	-0.114995	0.02323	-0.006228	0.00810
Cowlitz	0.005222	-0.018578	0.07109	-0.002259	0.00448
Toutle River	0.000001	-0.222393	0.94904	0.006347	0.05898
Washougal	0.000003	-0.059982	0.09285	-0.012545	0.00497

Table E.8: Results of the bivariate model with Summer average SST and the Northern upwelling extent for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 SumSST + \beta_2 Northexnt}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	Northern Upwelling Extent				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	48^o N Summer - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	$9.86\ 10^{-10}$	-0.108934	0.08034	-0.054866	0.04012
Lower Elwha	0.688889	0.195025	0.10242	0.076050	0.03923
Coastal:					
Soleduc	0.000039	-0.061675	0.16120	0.055401	0.09024
Quinault Lake	$1.70\ 10^{-10}$	-0.123539	0.01153	0.048229	0.01153
Quinault National Fish	$1\ 10^{-10}$	-0.203572	0.05571	-0.005102	0.03627
Humptulips	$1.38\ 10^{-10}$	-0.281080	0.09253	0.088029	0.04835
Simpson	$3.79\ 10^{-8}$	-0.086367	0.04565	0.039760	0.04565
Willapa	$2.04\ 10^{-10}$	0.003456	0.08068	-0.101892	0.06867
Lower Columbia					
Grays River	0.000190	-0.025592	-0.02592	0.122945	0.04727
Elochomin	$1.42\ 10^{-10}$	-0.162882	-0.16288	0.235930	0.12266
Cowlitz	0.072729	0.033386	0.03339	0.048892	0.03406
Toutle River	0.000003	-0.018921	-0.01892	0.044784	0.06519
Washougal	0.303867	0.073749	0.07375	0.036480	0.06053

Table E.9: Results of the bivariate model with Summer average SST and March - September cumulative upwelling at 45^{o} N for all hatcheries. The bivariate PH model is $(S_o)^{e^{\beta_1 SumSST + \beta_2 Cu45}}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	45^{o} N Cumulative Upwelling				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	45^{o} N Cumulative - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000232	-0.072455	0.07780	-0.000033	0.00045
Lower Elwha	0.003702	0.328945	0.09421	0.001401	0.00059
Coastal:					
Soleduc	$4.05\ 10^{-10}$	-0.097615	0.07132	-0.001350	0.00081
Quinault Lake	$4.08\ 10^{-21}$	-0.172251	0.07549	-0.000073	0.00037
Quinault National Fish	$8.31\ 10^{-54}$	-0.231466	0.03814	-0.000890	0.00030
Humptulips	$2.12\ 10^{-31}$	-0.198839	0.01414	-0.000661	0.00081
Simpson	$1.81\ 10^{-15}$	-0.139535	0.05003	-0.000889	0.00042
Willapa	$4.05\ 10^{-322}$	-0.375879	0.00950	-0.001000	0.00052
Lower Columbia					
Grays River	0.000539	-0.049689	0.08559	0.000686	0.00053
Elochomin	No standard error estimates of beta 1 available				
Cowlitz	0.044317	0.013600	0.07450	0.000061	0.00050
Toutle River	$4.08\ 10^{-7}$	-0.087887	0.09522	-0.000859	0.00072
Washougal	$1.32\ 10^{-9}$	-0.096057	0.07842	-0.001904	0.00045

Table E.10: Results of the bivariate model with Summer average SST and March - September cumulative upwelling at 48^{o} N for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 SumSST + \beta_2 Cu48}$, and models survival to age two.

Hatchery	SUMMER Sea Surface Temperature (SST)				
	48^{o} N Cumulative Upwelling				
	S_o	Summer SST - $\hat{\beta}_1$	se($\hat{\beta}_1$)	48^{o} N Cumulative - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000187	-0.080813	0.07408	0.000659	0.00056
Lower Elwha	0.094246	0.300640	0.12995	0.001326	0.0010
Coastal:					
Soleduc	$5.62\ 10^{-5}$	-0.061054	0.15879	0.000310	0.00122
Quinault Lake	$6.53\ 10^{-43}$	-0.217088	0.07760	-0.000846	0.00056
Quinault National Fish	$5.33\ 10^{-42}$	-0.215257	0.04460	-0.001168	0.00041
Humptulips	$2.42\ 10^{-148}$	-0.309853	0.11276	-0.001650	0.00080
Simpson	$3.79\ 10^{-8}$	-0.099872	0.04856	-0.000312	0.00048
Willapa	Did not converge				
Lower Columbia					
Grays River	$1.70\ 10^{-10}$	-0.116490	0.08363	-0.000287	0.00056
Elochomin	$3.26\ 10^{-81}$	-0.271088	0.12540	-0.000970	0.00093
Cowlitz	$7.54\ 10^{-5}$	-0.055155	0.06923	-0.001150	0.00064
Toutle River	0.027291	0.015230	0.08379	-0.001798	0.00058
Washougal	0.000109	-0.042599	0.07945	-0.002202	0.00063

Table E.11: Results of the bivariate model with Northern upwelling extent and June SST for all hatcheries. The bivariate PH model is $(S_o)^{e^{\beta_1 NorExt + \beta_2 JunSST}}$, and models survival to age two.

Hatchery	NORTHERN UPWELLING EXTENT				
	June temperature				
	S_o	Northern Extent - $\hat{\beta}_1$	se($\hat{\beta}_1$)	June SST - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.000800	-0.018038	0.03858	-0.059873	0.03350
Lower Elwha	0.247170	0.096750	0.04575	0.075656	0.05456
Coastal:					
Soleduc	0.000759	0.064009	0.05754	-0.045883	0.05813
Quinault Lake	0.002985	0.046084	0.03975	-0.033367	0.03796
Quinault National Fish	0.000090	0.010715	0.03796	-0.063568	0.03250
Humptulips	0.000061	0.063422	0.05073	-0.080226	0.05494
Simpson	0.000318	0.036176	0.03313	-0.058258	0.03074
Willapa	0.000002	0.003456	0.02258	-0.101892	0.08640
Lower Columbia					
Grays River	0.012689	0.118744	0.04292	-0.017623	0.03754
Elochomin	0.227559	0.236141	0.08920	0.036073	0.10226
Cowlitz	0.993943	- 0.21602*	*	0.66836*	*
Toutle River	0.153269	0.119270	0.03585	0.025274	0.04751
Washougal	1.000*	8.355746*	*	0.358907*	*

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient averages

Table E.12: Results of the bivariate model with Northern upwelling extent and the North Pacific Index (NPI) for all hatcheries. The bivariate PH model is $(S_o)^{e^{\beta_1 NorExt + \beta_2 NPI}}$, and models survival to age two.

Hatchery	NORTHERN UPWELLING EXTENT				
	North Pacific Index (NPI)				
	S_o	Northern Extent - $\hat{\beta}_1$	se($\hat{\beta}_1$)	NPI - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.024046	-0.049277	0.032390	0.054010	0.01218
Lower Elwha	0.008464	-0.003087	0.041490	0.039477	0.01795
Coastal:					
Soleduc	0.023458	0.071711	0.055910	-0.016337	0.01911
Quinault Lake	0.025714	0.055275	0.045830	-0.007036	0.01429
Quinault National Fish	0.019558	0.014209	0.041380	-0.015466	0.01167
Humptulips	0.051600	0.128967	0.067820	-0.042032	0.02284
Simpson	0.027911	0.066068	0.041170	-0.013120	0.01244
Willapa	0.037825	0.034686	0.099740	-0.004771	0.02550
Lower Columbia					
Grays River	0.043734	0.162870	0.057920	-0.014417	0.01480
Elochomin	0.151155	0.332769	0.083170	-0.057421	0.02405
Cowlitz	0.057610	0.121104	0.038315	-0.036542	0.01227
Toutle River	0.037437	0.047282	0.050770	-0.071800	0.02541
Washougal	0.058268	0.105798	0.091620	-0.029111	0.02404

Table E.13: Results of the bivariate model with Northern upwelling extent and the Pacific Northwest Index (PNI) for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 NorExt + \beta_2 PNI}$, and models survival to age two.

Hatchery	NORTHERN UPWELLING EXTENT				
	Pacific Northwest Index (PNI)				
	S_o	Northern Extent- $\hat{\beta}_1$	se($\hat{\beta}_1$)	**PNI** - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.023970	-0.057353	0.03594	-0.119220	0.04663
Lower Elwha	0.019121	0.086073	0.04947	-0.008717	0.06465
Coastal:					
Soleduc	0.019370	0.057789	0.05491	0.001423	0.02892
Quinault Lake	0.029242	0.046668	0.03530	0.106760	0.04641
Quinault National Fish	0.018473	-0.002033	0.02145	0.086226	0.03644
Humptulips	0.037149	0.062880	0.05053	0.097267	0.06185
Simpson	0.029328	0.073736	0.05758	0.082407	0.03128
Willapa	0.002989	-0.145232	0.10000	-0.541939	0.16908
Lower Columbia					
Grays River	0.026616	0.111911	0.05134	-0.041341	0.06662
Elochomin	0.159267	0.354834	0.09638	0.160841	0.07402
Cowlitz	0.993548	1.490824*	*	0.807131*	*
Toutle River	0.083958	0.168890	0.06975	0.131657	0.04833
Washougal	0.032622	0.025394	0.06328	0.006236	0.07607

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient averages

Table E.14: Results of the bivariate model with Northern upwelling extent and June Upwelling at 45^{o} N for all hatcheries. The bivariate PH model is $(S_o)^{e^{\beta_1 NorExt + \beta_2 June45up}}$, and models survival to age two.

Hatchery	NORTHERN UPWELLING EXTENT				
	45^{o} N June Upwelling				
	S_o	Northern Extent - $\hat{\beta}_1$	se($\hat{\beta}_1$)	45^{o} N June - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.036044	-0.038661	0.04200	0.000194	0.00126
Lower Elwha	0.016951	0.142244	0.05275	-0.004239	0.00257
Coastal:					
Soleduc	0.022699	0.034507	0.05771	0.002225	0.00226
Quinault Lake	0.022560	0.049488	0.05314	-0.000298	0.00194
Quinault National Fish	0.020825	-0.029012	0.03974	0.002489	0.00117
Humptulips	0.034575	0.022841	0.05755	0.002578	0.00275
Simpson	0.024154	0.028719	0.04049	0.000910	0.00108
Willapa	0.036920	0.012053	0.10845	0.000972	0.00437
Lower Columbia					
Grays River	0.030651	0.150284	0.05079	-0.001406	0.00142
Elochomin	0.113963	0.171588	0.08452	0.004657	0.00283
Cowlitz	0.994088	2.167540*	*	-0.03064*	*
Toutle River	0.036639	0.134737	0.06759	-0.003581	0.00147
Washougal	0.031743	0.025642	0.06384	-0.000114	0.00142

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient averages

Table E.15: Results of the bivariate model with Northern upwelling extent and Summer Upwelling at 45^o N for all hatcheries. The bivariate PH model is $(S_o)^{e^{\beta_1 NorExt + \beta_2 Sum45up}}$, and models survival to age two.

Hatchery	NORTHERN UPWELLING EXTENT				
	45^o N Summer Upwelling				
	S_o	Northern Extent - $\hat{\beta}_1$	se($\hat{\beta}_1$)	45^o N Summer - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.067008	-0.044091	0.03850	0.005894	0.00405
Lower Elwha	0.011882	0.118946	0.06014	-0.004331	0.00564
Coastal:					
Soleduc	0.014010	0.059827	0.05403	-0.002086	0.00622
Quinault Lake	0.026426	0.027265	0.06227	0.001700	0.00046
Quinault National Fish	0.015737	-0.003159	0.03213	-0.000622	0.00271
Humptulips	0.038548	0.036017	0.06406	-0.002655	0.00845
Simpson	0.013153	0.070659	0.04050	-0.004687	0.00345
Willapa	0.999999*	-83.0125*	*	2.467928*	*
Lower Columbia					
Grays River	1.00	1.45401*	*	0.208229*	
Elochomin	0.075700	0.249320	0.09194	-0.002810	0.00663
Cowlitz	0.993960	0.221194*	*	0.079542*	*
Toutle River	0.098274	-0.048818	0.06782	0.013570	0.00607
Washougal	0.008058	0.146412	0.05786	-0.012728	0.00319

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient averages

Table E.16: Results of the bivariate model with Northern upwelling extent and June Upwelling at 48^{o} N for all hatcheries. The bivariate PH model is $(S_o)^{e^{\beta_1 NorExt + \beta_2 Jun48up}}$, and models survival to age two.

Hatchery	NORTHERN UPWELLING EXTENT				
	48^{o} N June Upwelling				
	S_o	Northern Extent - $\hat{\beta}_1$	se($\hat{\beta}_1$)	48^{o} N June - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.036568	-0.039396	0.04132	0.000367	0.00162
Lower Elwha	0.016722	0.115867	0.04757	-0.003469	0.00259
Coastal:					
Soleduc	0.025318	0.019056	0.05406	0.004860	0.00280
Quinault Lake	0.022622	0.045229	0.04375	-0.000087	0.00146
Quinault National Fish	0.016898	-0.009380	0.03845	0.000723	0.00143
Humptulips	0.035144	0.028109	0.05297	0.002742	0.00249
Simpson	0.027328	0.012380	0.03730	0.003274	0.00153
Willapa	0.999981*	6.927009*	*	-0.128937	*
Lower Columbia					
Grays River	0.031115	0.147506	0.05066	-0.001319	0.00152
Elochomin	0.129000	0.236870	0.08209	0.004425	0.00485
Cowlitz	0.993905	1.718799*	*	-0.10304*	*
Toutle River	0.023290	0.040334	0.05835	-0.002818	0.00143
Washougal	1.00*	9.541464*	*	-0.00461*	*

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient averages

Table E.17: Results of the bivariate model with Northern upwelling extent and Summer average Upwelling at 48° N for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 NorExt + \beta_2 Sum48up}$, and models survival to age two.

Hatchery	**NORTHERN UPWELLING EXTENT**				
	48° N Summer Upwelling				
	S_o	Northern Extent - $\hat{\beta}_1$	se($\hat{\beta}_1$)	48° N Summer - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.066672	-0.015720	0.03804	0.006249	0.003420
Lower Elwha	0.021077	0.087903	0.04655	0.000670	0.006170
Coastal:					
Soleduc	0.054866	0.068579	0.04911	0.010539	0.004850
Quinault Lake	0.023109	0.044068	0.04141	0.000158	0.002510
Quinault National Fish	0.010289	-0.008989	0.03984	-0.003205	0.003050
Humptulips	0.023117	0.053196	0.05484	-0.002149	0.005660
Simpson	0.028082	0.041198	0.03599	0.002058	0.003090
Willapa	0.005419	0.159761	0.09373	-0.020671	0.007470
Lower Columbia					
Grays River	0.032953	0.127285	0.04528	0.000217	0.003350
Elochomin	0.843882	1.060375*	*	-0.02963*	*
Cowlitz	0.022086	0.050928	0.03346	0.003405	0.004076
Toutle River	0.000001	-0.30096*	*	-0.28242*	*
Washougal	0.006072	0.165336	0.05998	-0.019714	0.004710

* - Denotes inconsistent estimates that were not used in the weighted t-tests of coefficient average

Table E.18: Results of the bivariate model with Northern upwelling extent and March - September cumulative upwelling at 45° N for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 NorExt + \beta_2 Cu45}$, and models survival to age two.

Hatchery	NORTHERN UPWELLING EXTENT				
	45° N Cumulative Upwelling				
	S_o	Northern Extent - $\hat{\beta}_1$	se($\hat{\beta}_1$)	45° N Cumulative - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.042414	-0.038012	0.03836	0.000307	0.00072
Lower Elwha	0.018366	0.094478	0.05164	-0.000163	0.00067
Coastal:					
Soleduc	0.00730	0.072375	0.05302	-0.001348	0.00084
Quinault Lake	0.020810	0.072120	0.06069	-0.000394	0.00064
Quinault National Fish	0.012268	0.006519	0.04077	-0.000468	0.00029
Humptulips	0.019615	0.066896	0.05606	-0.000757	0.00091
Simpson	0.017322	0.062525	0.03774	-0.000582	0.00039
Willapa	0.037224	0.022746	0.09150	0.000131	0.00103
Lower Columbia					
Grays River	0.035322	0.118090	0.04888	0.000234	0.00053
Elochomin	Did not converge				
Cowlitz	0.024508	0.085777	0.04387	-0.000776	0.00059
Toutle River	0.026048	0.074117	0.05797	-0.000936	0.00070
Washougal	0.021540	0.246171	0.04737	-0.002949	0.00039

Table E.19: Results of the bivariate model with Northern upwelling extent and March - September cumulative upwelling at 48° N for all hatcheries. The bivariate PH model is $(S_o)e^{\beta_1 NorExt + \beta_2 Cu48}$, and models survival to age two.

Hatchery	NORTHERN UPWELLING EXTENT				
	48° N Cumulative Upwelling				
	S_o	Northern Extent - $\hat{\beta}_1$	se($\hat{\beta}_1$)	48° N Cumulative - $\hat{\beta}_2$	se($\hat{\beta}_2$)
Strait of Juan de Fuca					
Dungeness	0.045742	-0.027490	0.03910	0.000478	0.00059
Lower Elwha	0.019752	0.088498	0.08681	0.000006	0.99569
Coastal:					
Soleduc	0.023475	0.057334	0.05360	0.000434	0.00104
Quinault Lake	0.019384	0.057242	0.04424	-0.000501	0.00064
Quinault National Fish	0.008444	-0.007808	0.04262	-0.000994	0.00051
Humptulips	0.022561	0.056056	0.04914	-0.000607	0.00067
Simpson	0.022770	0.045160	0.03587	-0.000067	0.00041
Willapa	0.015044	0.179416	0.08681	-0.003503	0.00111
Lower Columbia					
Grays River	0.026722	0.148216	0.04936	-0.000661	0.00060
Elochomin	0.058190	0.217476	0.08151	-0.001292	0.00093
Cowlitz	0.019435	0.082439	0.03437	-0.001526	0.00060
Toutle River	0.010591	-0.008193	0.05204	-0.001803	0.00060
Washougal	0.016335	0.297588	0.06454	-0.004534	0.00075

Appendix F

Other Parameter Estimates

The values presented in this table were the typical values estimated for M_2, θ_1, and θ_2 from the CWT data. Since these parameters were estimated from the same statistics in all models, the estimates were approximately the same for all models.

Table F.1: A table showing the estimates of M_2, θ_1 , and θ_2.

Hatchery	M_2 estimate	θ_1	θ_2
Dungeness	0.0040	0.9999	0.0103
Lower Elwha	0.0564	0.9999	0.0032
Soleduc	0.1137	0.9999	0.0174
Quinault Lake	0.0843	0.9999	0.0014
Quinault NFH	0.0859	0.9999	0.0002
Humptulips	0.0282	0.9999	0.0006
Simpson	0.0116	0.9999	0.0226
Willapa	0.0364	0.9999	0.0015
Grays River	0.0650	0.9999	0.0015
Elokomin	0.0247	0.9999	0.0060
Cowlitz	0.1110	0.9999	0.0216
Toutle River	0.0097	0.9999	0.0007
Kalama Creek	0.0202	0.9999	0.0006
Kalama Falls	0.0105	0.9999	0.0043
Washougal	0.0043	0.9999	0.0052